THE SPAWNING MIGRATION OF CAPELIN (MALLOTUS VILLOSUS) IN ICELANDIC WATERS

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The spawning migration of capelin (*Mallotus villosus*) in Icelandic waters.

By

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Thesis abstract

Capelin (*Mallotus villosus*) is one of the most important commercial fish stocks in Icelandic waters and a major forage species as important prey for predatory fish, sea birds and marine mammals. Capelin have adapted to the sub-arctic environment by migrating north (67–72°N) to feed during summer in deep cold waters (>500m; 1–3°C) before migrating south (63–65°N) in winter to spawn in warmer shallow waters (<100m; 5–7°C) on the south and west coasts of Iceland. To examine mechanisms regulating location and timing of the spawning migration, acoustic recordings were analyzed from capelin winter acoustic assessment surveys from thirteen cohorts spawning in 1992-3, 1995, and 1998 to 2007.

The southward capelin spawning migration of all studied cohorts (from 63-67°N) utilized a consistent route within southward flowing cold sub-arctic waters (1–3°C) off the east coast of Iceland. Migration was not passive but active. The route followed the outer shelf edge but was beyond it (>200m bottom depth). Further south (<65°N), after the front with warmer Atlantic waters (>4.5°C) was encountered, the migration route veered inshore (<200m bottom depth) towards coastal spawning grounds.

The annual spawning migration moved southward across latitude 67°N between December 23 to January 20 in all years. Both an increased spawning biomass and colder summer feeding temperatures resulted in earlier migration. The migration was not continuous but staged, with a staging area located offshore in the transition zone between the offshore and the inshore phase of the migration (63.8-65.8°N). Capelin amassed in the staging area until roe content reached 12–14%.

Several mechanisms are involved in the migration. The movement southward appears to be innate, but the route tracks an offshore thermal corridor until reaching the Atlantic Ocean front. Capelin then stage in the warmer waters until gonad maturity reaches a roe content of 12–14% before moving inshore towards the spawning grounds. The dependence on temperature suggests that warming temperatures north of Iceland (to >4.5°C) could result in capelin spawning grounds shifting north as occurred in the 1930's. The extended migration route over deep waters seaward of the shelf edge and the act of staging may have evolved to minimize the period of spatial overlap with cod (and hence predation) that occurs on the shelf.

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Symbol	Description	Units
	Chapter 3	
TS	Target strength	dB
L	Total body length of fish	cm
	APPENDIX I	
S_a	Area backscattering strength	dB
$\delta S_{a200\text{-}120}$	Frequency difference in area backscattering strength	dB
s_a	Area backscattering coefficient	-
$\log(s_a)$	Logarithm of area backscattering coefficient	-
max S_v	Maximum volume backscattering strength	dB
mean S_v	Mean volume backscattering strength	dB
st.dev.(s_a)	Standard deviation of area backscattering coefficients	-
log(st.dev.(s_a))	Logarithm of the standard deviation of area backscattering coefficients	-

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Chapter 1. Introduction and Overview

1.1 Biology and ecology of capelin (*Mallotus villosus*)

Capelin (*Mallotus villosus*) is a coldwater smelt (family *Osmeridae*) with circumpolar distribution in the northern oceans (Carscadden and Vilhjálmsson, 2002). This small (< 20 cm), pelagic, plankton-feeding, schooling fish is a keystone species in the boreal food web (Carscadden *et al.*, 2001; Dolgov, 2002; Vilhjálmsson, 2002). Capelin is an important prey for various predatory fish (e.g. Dolgov, 2002; Vilhjálmsson, 2002), marine birds (e.g. Lilliendahl and Solmundsson, 1997; Davoren *et al.*, 2003) and marine mammals such as whales and seals (e.g. Piatt and Methven, 1992; Stenson *et al.*, 1997). It is well documented how capelin affects the vital rates and distribution of its many predators, especially Atlantic cod (*Gadus morhua*) (Nakken, 1994; Rose and O'Driscoll, 2002; Vilhjálmsson, 2002; Hylen *et al.* 2008; Pálsson and Björnsson, 2011).

Several stock complexes occupy the Barents Sea (Gjøsæter, 1998), the shelf of Newfoundland and Labrador including the Gulf of St. Lawrence (Templeman, 1948), Greenland waters (Friis-Rødel and Kanneworff, 2002), the Gulf of Alaska as well as the Bering Sea (Brown, 2002), Sea of Okhotsk (Velikanov, 2002) and Icelandic waters (Vilhjálmsson, 1994). The large stocks occupying the Barents Sea and Icelandic waters are commercially important with variable catches that in some years reach 3 (ICES, 2010) and 1.6 million metric tonnes (Anon, 2011), respectively.

Capelin is short lived with the majority dying after spawning at two to five years of age (Vilhjálmsson, 1994). During their short life they migrate between geographically separated spawning, nursing, over-wintering and feeding grounds (Templeman, 1948; Vilhjálmsson, 1994; Gjøsæter, 1998; Friis-Rødel and Kanneworff, 2002). The distribution and migration ranges vary among the stock complexes. Capelin in Greenland

has a small distribution range as they remain within a single fjord for the entire life cycle (< 50 km; Friis-Rødel and Kanneworff, 2002). In contrast, the Icelandic capelin has a large distribution range and a complete migration cycle that spans approximately 2000 km (Vilhjálmsson, 1994).

The abundance and distribution of the Icelandic capelin stock have been recorded annually since the late 1970s using hydro-acoustics (Vilhjálmsson, 1994). Capelin behaviour limits application of acoustic measurements in spring and summer when densities are low and fish are located near the surface. In fall and winter, however, capelin aggregate and move deeper in the water column where the acoustic beam can record them. In most years acoustic surveys are conducted in fall and in winter (Vilhjálmsson and Carscadden, 2002). In the fall, both juvenile and maturing capelin are measured, providing preliminary estimates of expected abundance in the coming year. In most years, however, the fall survey results do not provide a comprehensive stock estimate for various reasons, including stormy weather, abnormal or scattered distribution and ice conditions. In some years, the abundance estimate in the fall is far below expectations and thus contested by the fishing industry (Vilhjálmsson and Carscadden, 2002). By winter (January), with the spawning migration beginning, the fish become more densely aggregated and typically confined to a small area on or in the vicinity of the continental slope thus providing prime conditions for acoustic surveying (Vilhjálmsson, 1994). The winter surveys concentrate on measuring the spawning stock.

Capelin is one of the more valuable commercial species in Iceland with an annual landed values as high as $ 143 million CAD (www.hagstofa.is). The fishery is focused on pre-spawning fish with the majority of the fishing effort occurring during the spawning

migration (Vilhjálmsson, 2002). The management strategy is to have a minimum of 400,000 metric tons of capelin spawning each year with the excess biomass available to the fishery (Gudmundsdottir and Vilhjálmsson, 2002). Precise annual abundance estimates are critical to the success of this strategy as the stock is renewed annually and recruitment is highly variable (Anon, 2011). Surveying begins in the fall and continues in winter if the biomass cannot be estimated. Research vessel(s) search to the north and east of Iceland until the spawning migration is located and capelin abundance can be measured. Surveying begins in October and can continue until late March.

Decades of acoustic surveys have revealed the general migration pattern of the Icelandic capelin stock. The migration begins in the fall in Arctic waters north of Iceland and ends at the spawning grounds in coastal waters south and west of Iceland in February to April (Fig. 1.1) (Vilhjálmsson, 1994). Spawning is limited to shallow coastal areas (< 100 m) and occurs mostly between 30 – 50 m. Capelin attach their eggs to the bottom substrate (Thors 1981; Vilhjálmsson, 1994) with eggs hatching in approximately three to four weeks (Friðgeirsson, 1976). The newly hatched larvae drift with surface currents clockwise around the island. By August, the larvae are west, north or east of Iceland, mostly located within the continental shelf area (Vilhjálmsson, 1994). Typically, juveniles move further offshore and are generally found on the shelf edge, northwest, north and northeast of Iceland and in some years on the East Greenland shelf (Vilhjálmsson, 1994). In the early 2000s, the distribution of juvenile capelin changed drastically as they appear to have abandoned their traditional distribution area (Anon, 2011). Nevertheless, these co-called "lost" year classes, 2001-2008, utilized the

traditional spawning grounds as they matured a few years later. Their location as juveniles remains unknown (Anon, 2011).

Every spring capelin that will spawn during the next year migrate north into the Iceland Sea to feed during the short but highly productive Arctic summer. Capelin weight increases 2 to 4 fold during the summer feeding period (Vilhjálmsson, 1994). The feeding migration that follows transfers large quantities of energy from the Arctic to the ecosystem of the Iceland shelf from the Iceland Sea. The northern range of the feeding migration varies between years with capelin reaching latitude 72 °N in warm years but limited to the area south of 68 °N in cold years (Vilhjálmsson, 1994, 2002). Juvenile capelin do not participate in the feeding migration. In fall, pre-spawning capelin are located along the shelf edge of the east coast of Greenland and on the continental slope northwest, north and northeast of Iceland. They are usually located further offshore than the immature stock (Vilhjálmsson, 1994).

In most years, maturing capelin migrate to their southern spawning grounds along the east coast of Iceland (Vilhjálmsson, 1994). Migratory capelin follow the continental slope north and east of Iceland in a clockwise manner until reaching latitudes of 64 – 65 °N off the southeast coast. At these latitudes capelin turn, head west onto the continental shelf and then enter shallow coastal waters following the coast clockwise around the island until they are ready to spawn.

Timing of the spawning migration is reported to vary. In early January, the recorded average location ranges from latitude 64° 20' to 67° 40' N, a difference of 400 km (Table 7.1 in Vilhjálmsson, 1994). The leading southern edge of the migration can reach latitude 64 °N anytime from the beginning to the end of January (Appendix I in

Vilhjalmsson, 1994), however, capelin have never been located in warm inshore waters before February (Vilhjalmsson, 1994). These reports suggest that the spawning migration of Icelandic capelin is not continuous. A staging area may exist offshore that is occupied prior to the final migration leg to the spawning grounds in shallow coastal waters.

There is another shorter and less used migration route that takes maturing capelin counterclockwise along the west coast to the same spawning grounds west and south of Iceland (Vilhjálmsson, 1994). The bulk of the spawning stock in 2001 used the western route, just one of 13 cohorts investigated. Additionally, in some years a small fraction, 1-28%, of the spawning stock uses the western route. There is no explanation as to why maturing capelin used the western route in some years.

Temperature affects the distribution of capelin (Rose, 2005). In general, capelin spawn in warmer waters than they otherwise occupy (Templeman, 1948; Thors, 1981; Gjøsæter and Loeng, 1987; Carscadden *et al.*, 1989; Stergiou, 1989; Vilhjálmsson, 1994). The Icelandic capelin stock spawns in waters having 5 to 7 °C temperatures (Thors, 1981; Vilhjálmsson, 1994), which is several degrees warmer than their feeding range of -1 to 3 °C (Vilhjálmsson, 1994). The largest known shift in the last decades occurred on the Newfoundland shelf with capelin shifting their feeding and over-wintering distribution south to the Scotia shelf and east to the Flemish Cap in the late 1990s in association with colder than normal conditions (Frank *et al.*, 1996). In Icelandic waters, temperature changes have influenced both feeding distributions and spawning locations (Saemundsson, 1934; Vilhjálmsson, 1994, 2002). Changes in summer feeding migrations are related to the variable location of the southern boundary of the Arctic front, which ranges from 72 °N in warm years to 68 °N in cold years (Vilhjálmsson, 1994, 2002).

Changes in capelin spawning grounds are more extreme. During a few consecutive years in the 1930s the spawning grounds shifted to the north coast of Iceland from their traditional location along the south and west coast of Iceland (Saemundsson, 1934). During this time temperatures on the north coast were 3 to 4 °C warmer than normal (Saemundsson, 1934). At the same time, temperatures on the traditional spawning grounds along the south and west coast of Iceland were only approximately 1 °C warmer than normal (Saemundsson, 1934).

Barents Sea capelin are also known to modify both their northern feeding range and spawning areas to mirror temperature fluctuations. The summer feeding migration follows the polar front which is located further north in warmer years (Ozhigin and Luka, 1984). Furthermore, capelin spawning grounds shift east in warmer years (Ozhigin and Luka, 1984).

1.2 Study region

Iceland is located near the Arctic circle, latitude 63 – 67 °N. The island forms the top of a volcanic shelf that rises from the Greenland – Iceland – Faroe Ridge which separates the cold waters (< 0 to 3 °C) of the Nordic Seas from the warm waters (5 – 9 °C) of the northeast Atlantic (Fig. 1.2) (Blindheim and Østerhus, 2005). Mixing of these water masses is limited to sills southeast (64 °N) and northwest (66 °N) of Iceland, hence, the west coast is bathed in warm waters whereas the east coast has much colder conditions (Blindheim and Østerhus, 2005). The continental shelf covers approximately 212,000 km^2 within the 500 m depth contour and extends from 110 to 170 km from the coast to the west, north and east of Iceland. In the south it is narrower. The continental slope is

steep except at the junction with the Greenland – Iceland – Faroe Ridge with deep ocean basins both south and north of Iceland.

Several distinctive surface currents are found around Iceland (Fig. 1.2). The cold currents are the East Greenland Current (polar water of < 0 °C) and the East Iceland Current (Arctic water of 1 – 3 °C) (Malmberg *et al.*, 1996). Both currents flow southwards from the Arctic with the East Greenland Current flowing along the coast of Greenland and the East Iceland current flowing clockwise along the shelf slope of the north and northeast coast of Iceland. The Irminger Current, a back-eddying branch of the warm North Atlantic Drift, flows westwards along the south coast and northwards along the west coast, then onto the shelf north of Iceland where it deteriorates as it mixes with the East Iceland Current. The strength of the Irminger Current is highly variable among years causing variable hydrographic conditions on the shelf north of Iceland (Malmberg *et al.*, 1996; Jónsson and Valdimarson, 2005). In addition to these large oceanic currents, there is a coastal current running clockwise around the island (Stefánsson and Ólafsson, 1991).

The marine ecosystems north and south of Iceland are very different due to diverse oceanography. The warmer south has higher primary (Gudmundsson, 1998) and secondary production (Gislason and Astthorsson, 2004) and greater fish biomass (Anon, 2011). Most of the approximately 25 exploited fish species within the Icelandic Economic Exclusion Zone have their major spawning grounds south of Iceland and nursing and juvenile grounds to the north (Marteinsdottir *et al.*, 2000; Jónsson and Pálsson, 2006; Armannsson *et al.*, 2007; Brickman *et al.*, 2007).

The boreal ecosystem of Icelandic waters is species poor with a few dominant species and strong interactions through predation (Astthorsson *et al.*, 2007). There are strong seasonal cycles in primary and secondary production (Gudmundsson, 1998; Astthorsson *et al.*, 2007), especially to the north. During the short but intense Arctic summer, the Iceland Sea (67 – 72 °N) provides prime feeding conditions for plankton feeding fish (Astthorsson and Gislason, 1997; Gislason and Astthorsson, 1998; Gudmundsson, 1998).

1.3 Fish migrations at high latitudes

Migration is an annual cyclic movement of a fish stock between geographically separated spawning, nursing and adult areas (Harden-Jones, 1968). Migrations play an important role in the ecology of boreal ecosystems as many species have developed strategies to maximize growth, survival and reproduction in seasonally changing northern oceans (e.g. Ozhigin and Luka, 1984; Rose, 1993; Vilhjálmsson, 1994, 2002; Dragesund *et al.*, 1997). At high latitudes, the strong seasonal variation in solar radiation creates seasonal blooms in epipelagic layer plankton production that drives fish feeding conditions (Sigurdsson and Astthorsson, 1991; Gjøsæter, 1998; Dalpadado *et al.*, 2000) and spans a wide range of temperatures (Jónsson, 2007). Furthermore, habitat preferences of fish change with life history stages. For example, pelagic feeding habitat of capelin and herring differs fundamentally from their benthic spawning habitat (Jakobsson, 1969; Gjøsæter, 1998; Jakobsson and Stefánsson, 1999; Vilhjálmsson, 2002).

In the northern oceans, many different patterns in migration routes and timing exist (Harden-Jones, 1968). Migration patterns often differ among species occupying the

same ecosystem (Vilhjálmsson, 2002; Óskarsson *et al.*, 2009) and between stocks (reproductively isolated unit in space or time) of the same species occupying different ecosystems (Tempelman, 1948; Dragesund *et al.*, 1997; Vilhjálmsson, 2002; Óskarsson *et al.*, 2009). A stock can have one major migration route (Vilhjálmsson, 1994) or many (Carscadden *et al.*, 1989; Gjøsæter, 1998). Generally, migration routes remain constant over periods of years or even decades (Vilhjálmsson, 1994; Dragesund *et al.*, 1997; Óskarsson *et al.*, 2009), however, abrupt changes in migration patterns can occur (Saemundsson, 1934; deYoung and Rose, 1993; Frank *et al.*, 1996; Dragesund *et al.*, 1997; Rose *et al.*, 2011).

Scientists have long been fascinated by the guiding mechanisms of fish migrations. Despite years of study, the sensory organ(s) and mechanisms used for navigation remain largely unknown. However, numerous factors have been linked to location of migration routes. Temperature is one of the best known. Some migration routes tend to follow a constant temperature range (Rose, 1993; Misund *et al.*, 1996), others avoid unfavorable temperature (Ozhigin and Luka, 1984; Frank *et al.*, 1996). Furthermore, ocean currents (Healey, 2000; Agostini *et al.*, 2006) and fronts (Hassel *et al.*, 1991; Jakobsson and Østvedt, 1996; Misund *et al.*, 1996), topography (Makris *et al.*, 2006), predation (McQuinn, 2009) and feeding conditions (Kvamme *et al.*, 2003) can influence migration routes. Also, the migration routes utilized may be stock density dependent (Dragesund *et al.*, 1997) or independent (Óskarsson *et al.*, 2009).

Migration cue mechanisms synchronize fish movement with future environmental conditions hundreds or thousands of kilometers away. Factors both extrinsic and intrinsic to the fish have been linked to migration timing. Temperature can influence migration

timing directly (Ozhigin and Luka, 1984; Quinn and Adams, 1996; Carscadden *et al.*, 1997; Hodgeson and Quinn, 2002) or indirectly, mediated by growth (Shackell *et al.*, 1994; Carscadden *et al.*, 1997). Intrinsic factors like somatic growth (Shackell *et al.*, 1994; Carscadden *et al.*, 1997), gonad development (Shackell *et al.*, 1994) and hormonal balance (Comeau *et al.*, 2001) also affect migration timing.

Staging areas are locations were migratory animals delay their migration and are well known in the more visible bird migrations, are not extensively documented in fishes. Staging has been recorded in a few salmonid species (*Oncorhynchus nerka, O. tshawytscha*) that undertake long-distance spawning migrations (Hodgson and Quinn, 2002; Mundy and Evenson, 2011). Davoren *et al.* (2006) reported that maturing migratory capelin on the Newfoundland shelf utilized the same staging area for several consecutive years. The role of staging in fish migrations is poorly understood.

Inherited traits are an important part of the evolution and maintenance of migration patterns (Hansen and Jonsson, 1991; Quinn *et al.*, 2000). In contrast, sudden changes in migration timing (Carscadden *et al.*, 1997) or pattern (Frank *et al.*, 1996) imply environmental effects. Not all environmental changes, however, lead to changes in migration changes. Environmental effects can be countered by conservatism, in which a year class follows the same migration pattern for life independent of environmental variability (Corten, 2002). Fish migrations are a complicated interaction between innate genetic factors and environmental forcing.

1.4 Hydro-acoustics

Physical properties of sound waves have been used as "underwater eyes" by scientists for almost a century (Sund, 1935). In simple terms, a directional beam of acoustic pulses is transmitted into the water and any changes in density within the acoustic beam, such as caused by an ensonified target, will reflect energy back to the source where the strength of the "backscatter" is measured. During the last decades major advances in scientific equipment, backscattering theory and data analysis have made acoustics a common tool for fishery research and survey estimates of distribution and abundance of fish (Simmonds and MacLennan, 2005). In addition to echo strength, a myriad of other properties may be measured, such as vertical depth and acoustic size of targets and location and properties of the sea bottom. Various echo energy and echo morphology variables are also recorded. Today, application of several different frequencies simultaneously is common in an attempt to collect as much information as possible from the target. Target strength differs with sound frequency (Foote, 1985) but not universally, hence frequency responses can be utilized to identify target species. Higher frequencies have higher resolution but shorter range due to increased absorption of the signal power (Simmonds and MacLennan, 2005).

Technical advances have facilitated application of hydro-acoustic methods to several disciplines related to fishery research. To name a few, it is now used to map distribution of aquatic macrophytes (Maceina and Shireman, 1980; Thomas *et al.*, 1990; Sabol *et al.*, 2002), chart bottom topography (Wilson *et al.*, 2007), identify bottom substrates and classify benthic habitats (Kenny *et al.*, 2003), and measure the abundance

and distribution of phytoplankton (Kim *et al.*, 2010) and zooplankton (Stanton *et al.*, 1994).

Despite the major advances in hydro-acoustic methods, identification and classification of backscatter remains a major challenge (Simmonds and MacLennan, 2005). Independent verification of species and size is typically required, utilizing a biological sample (McClatchie *et al.*, 2000) or in some cases underwater video (Sawada *et al.*, 2009). Nevertheless, some acoustic classifications of targets, especially in species poor ecosystems have proven successful. The first studies attempted to separate fish targets using single frequency echo energy and morphology data. Identification success increased with increasing differences in the acoustic properties of the fish targets (Rose and Leggett, 1988; Scalabrin *et al.*, 1996). More recently, classification algorithms using image of shape analysis (Haralabous and Georgakarakos 1996; LeFeuvre *et al.*, 2000), and using different frequencies simultaneously (Korneliussen *et al.*, 2009) have been attempted. Fish backscatter has been successfully separated from zooplankton (Madureira *et al.*, 1993; Kang *et al.*, 2002). Different zooplankton species can be identified (Brierley *et al.*, 1998) and some advances have been made in identifying acoustically similar fish species (Korneliussen *et al.*, 2009). Classification success increases if echo morphology is included (Woodd-Walker *et al.*, 2003).

In practice, assigning backscatter to species is usually done manually, based on a holistic synthesis of catch data and echo characteristics. It is a labor intensive process demanding extensive experience where biological sampling along with previous knowledge of the species-specific depth along with echo amplitude and morphology are

used (Simmonds and MacLennan, 2005). For now, automated systems remain in the research domain!

In fish, the source of most of the backscattered energy is the gas filled swim bladder (Foote, 1980). Species that do not have bladders, or have small or deflated bladders, have much lower target strengths (backscatter less energy). Integrated backscatter is converted into fish abundance using a target strength model that relates backscatter to length (or a derivation in weight). The equation is species specific (Foote, 1980) and sometimes stock specific (for capelin see Table 1.1). Information, in addition to fish distribution and abundance, can be derived from acoustic recordings. Fish size can be estimated from target strength data (McClatchie *et al.,* 1996). Fish swim speed and direction of movement can be calculated (Rose *et al.,* 1995). When sequential recordings are possible, a comprehensive picture of fish aggregation movements on daily or longer time scales can be derived (Rose, 1993).

Capelin is a prime candidate for hydro-acoustic measurements for several reasons. They have a relatively large swim bladder and hence present a large acoustic signal (Jørgensen, 2003). Availability to the acoustic beam and measurement success of capelin are related to their pelagic life cycle and typically and migrating behavior in large dense mono-species aggregations (Vilhjálmsson, 1994).

1.5 Thesis overview

In this thesis, I explore several aspects of the timing and route of the spawning migration of the Icelandic capelin stock. All available digitized acoustic data from capelin winter acoustic assessment surveys conducted by the Marine Research Institute (MRI) in

Reykjavik, Iceland, are used. Migration route and migration timing of 13 capelin cohorts spawning in 1992 to 1993, 1995, 1998 to 2007 were investigated. The survey design has a flexible time frame that differs from most scientific surveys as the survey continues until the pre-spawning migration is located and abundance measured. Annual winter survey effort has varied from none, as a consequence of a large spawning cohort being measured during the preliminary research in the fall, to surveys spanning several months when the spawning migration was late or abundance was unexpectedly low. I participated in the surveys in 2000 and 2001 as a research technician employed by the MRI and as a PhD student in 2006 and 2007.

In chapter III, I investigated the geographical location of capelin spawning migrations in Icelandic waters during winter (January to March). Major and minor migration routes were documented, with capelin using the major route in twelve of thirteen years investigated. The major route was located seaward of the continental shelf off the east coast of Iceland. Capelin actively swam with the currents along the shelf edge before migrating inshore to the spawning grounds further south. I show how location of the major spawning migration route was influenced by bathymetry, temperature and possibly cod predation.

The timing of the capelin migration on the eastern spawning migration route and the possible existence of a staging area were explored in chapter IV. I found that spawning stock biomass and temperature on the feeding ground correlated with the start of the spawning migration. In addition, the existence of a staging area offshore in the southern part of route was established. Finally, I describe how female gonad maturity surpassed a specific threshold before capelin migrated inshore towards the spawning

grounds. I suggest offshore staging provides a refuge from cod predation as cod distribution is limited to the shelf area.

As a biologist with limited hands-on experience applying and operating hydro-acoustic equipment I conducted a small study in Smith Sound, Newfoundland, reported in Appendix I. I tested two methods to differentiate backscatter from kelp (order *Laminariales*) and juvenile cod (*Gadus spp.*). Frequency responses (120 and 200 kHz) in backscatter did not differ. Predictive discriminant analysis of energetic parameters was successful in 91 % of cases.

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1.7 Tables

Table 1.1. Target strength (TS) of various capelin stocks measured with 38 kHz transducer. L = total length of fish in cm.

Capelin stock	TS equation	Reference
Iceland	$TS = 19.1 * \log_{10}(L) - 74.5$	Vilhjálmsson (1994)
Barents Sea	$TS = 19.1 * \log_{10}(L) - 74.0$	Drommasnes and Røttingen (1985)
Newfoundland and Labrador	$TS = 20.0 * \log_{10}(L) - 73.1$	Rose (1998)*
North Pacific Ocean	$TS = 20.0 * \log_{10}(L) - 70.3$	Guttormsen and Wilson (2009)

* Measured at 38 kHz and 49 kHz.

1.8 Figures

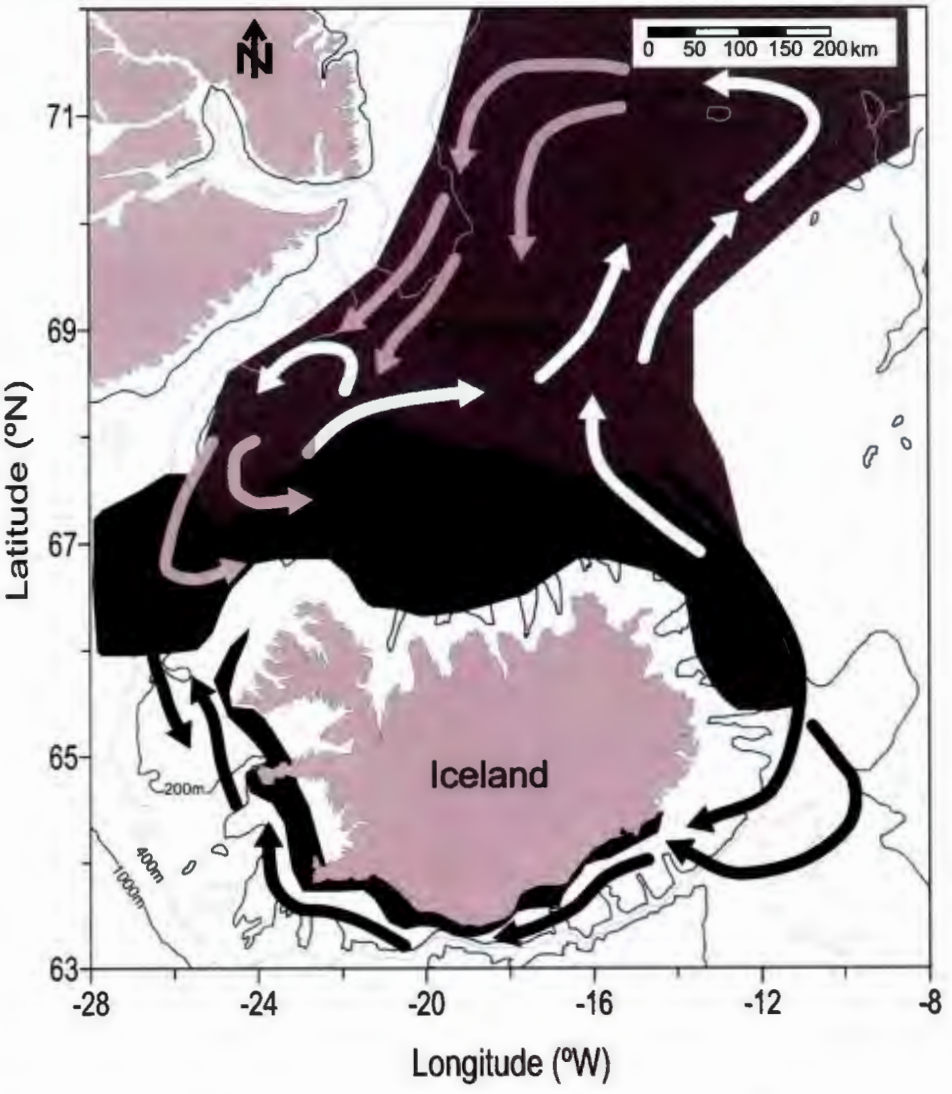

Figure 1.1. Distribution of various life history stages of the Icelandic capelin stock and migration routes of maturing capelin. In spring, maturing capelin migrate north (white arrows) to feed (light grey area) during summer, return south in fall (grey arrows) and begin the final leg of their journey, the spawning migration, in January (black arrows). The newly hatch larvae drift with surface currents from the spawning grounds (black area) to the nursing grounds (dark grey area). Figure redrawn from Vilhjalmsson (2002).

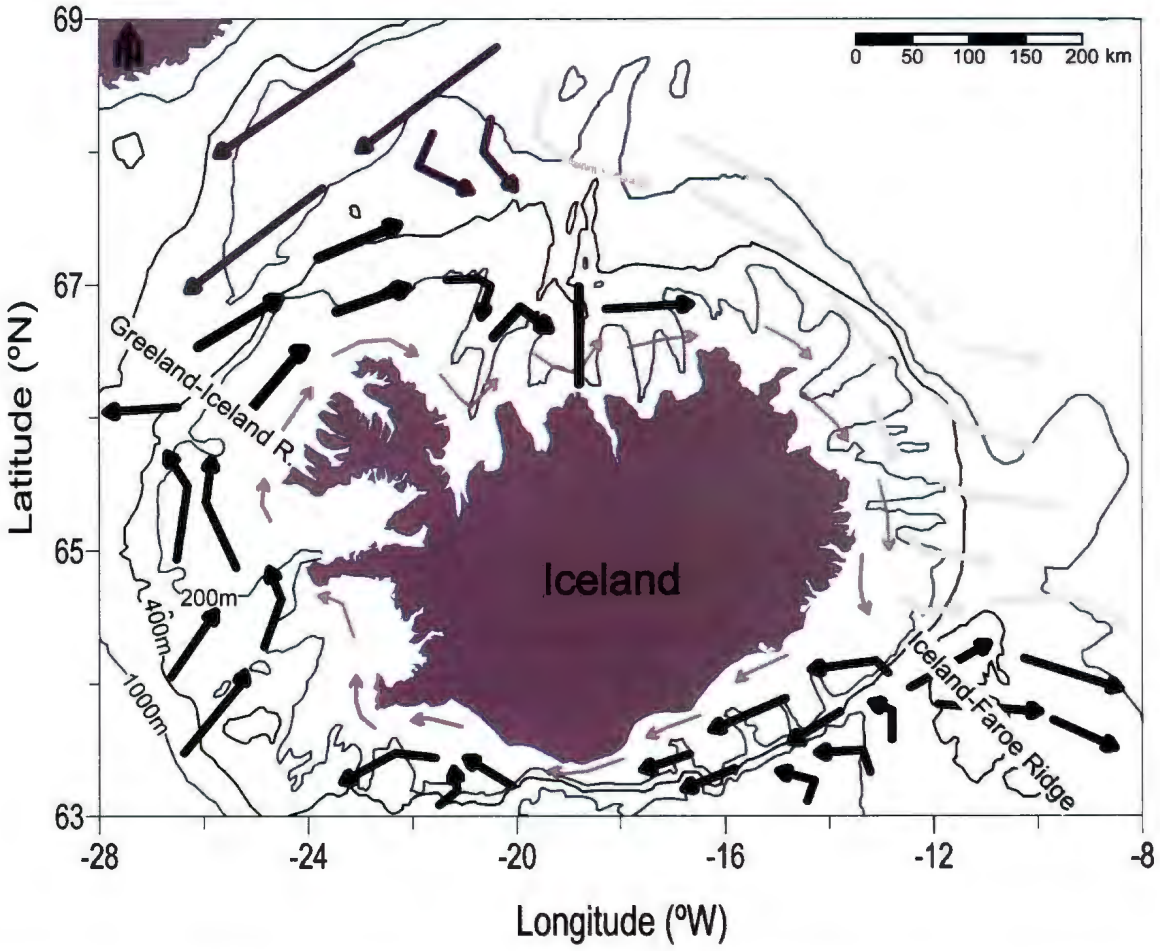

Figure 1.2. Surface currents and water masses around Iceland. Black arrows: The Irminger current (warm Atlantic water: 6-8 °C); light gray arrows: East Iceland Current (cold Arctic water: 1-3 °C); dark grey arrows: East Greenland Current (cold polar water: < 0 °C); narrow gray arrows: coastal current. Redrawn form Stefánsson and Ólafsson (1991).

Chapter 2. Co-authorship Statement

I am the main author of all research papers in this thesis. My work concentrated on utilizing acoustic recordings and biological samples from routine capelin abundance estimates surveys conducted by the Marine Research Institute, Reykjavik, Iceland. The data has never been analyzed in such detail before or connected to ambient oceanographic condition. I conducted all analysis with support from Dr. George A. Rose. Finally, I conceived and wrote all manuscripts with generous amounts of analytical and editorial comments from Dr. George A. Rose, who co-authors all manuscripts produced from this thesis.

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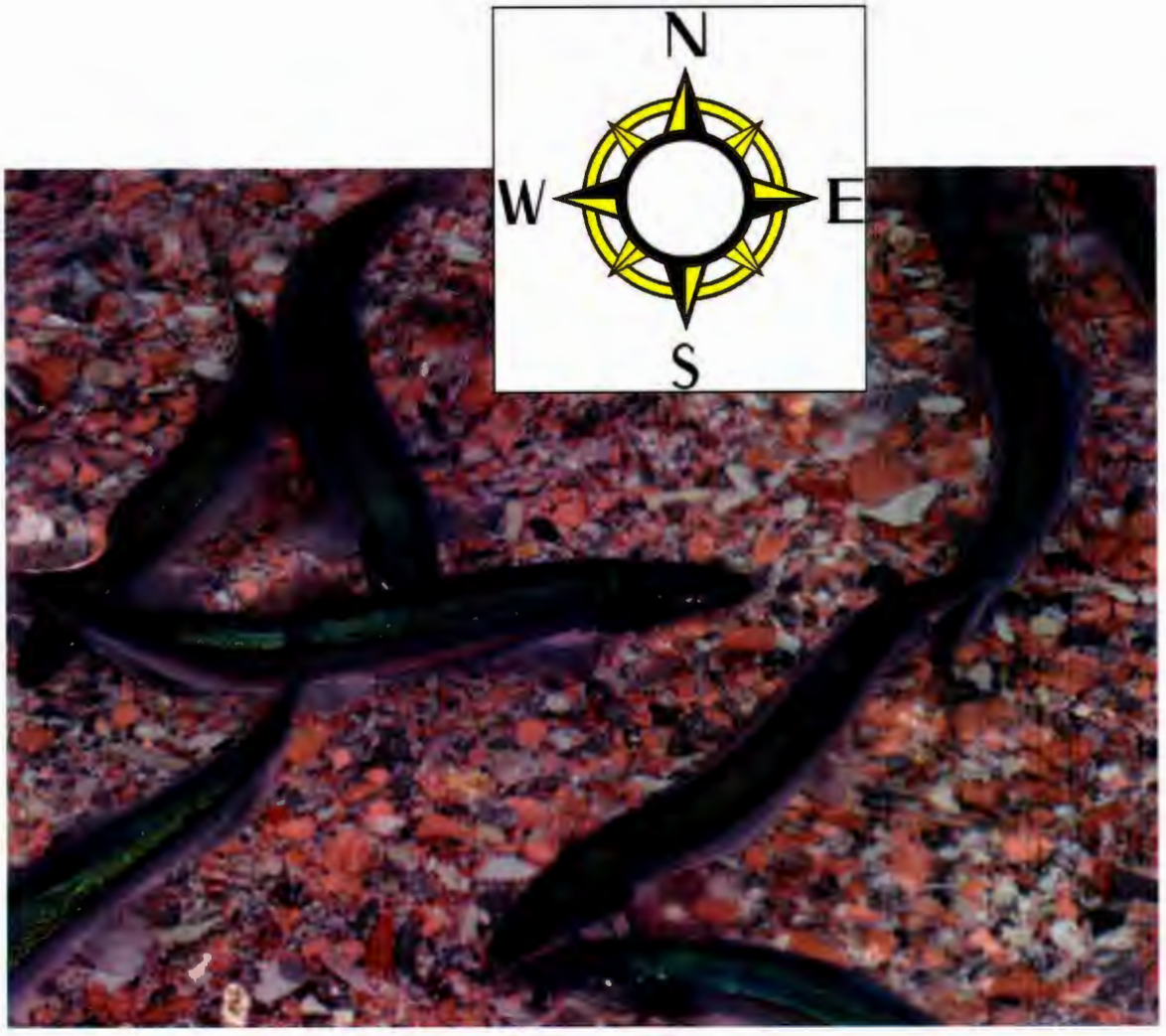
Chapter 3. Influences of temperature, bathymetry and fronts on spawning migration routes of Icelandic capelin (*Mallotus villosus*).



3.1 Abstract

Capelin (*Mallotus villosus*) is the largest commercial fish stock in Icelandic waters and also an important forage fish. Capelin have adapted to the sub-arctic environment by migrating north (67 – 72 °N) to feed during summer in deep cold waters (>500 m; 1–3 °C) before migrating south (63 – 65 °N) to spawn in winter in warmer shallow waters (<100 m; 5-7 °C) on the south and west coasts of Iceland. Hydro-acoustic data on capelin spawning migrations from 1992 to 2007 revealed a consistent southward route along which capelin migrated actively (ground velocity faster than current velocity) off the east coast (and a lesser used route off the west coast). North of 65 °N, the dominant eastern route followed the bathymetry, skirting the shelf edge (> 200 m bottom depth) within a funnel of near constant temperatures (ca. 2.5 °C). Further south, between 65 and 64 °N, as temperatures warmed to 4.5 °C (reaching 7.9 °C at 63.5 °N), capelin abruptly moved onto the shelf and towards the coastal spawning areas. Capelin spawning migrations appear to be an innately based southward search for appropriate spawning locations, guided by bathymetry and temperature. I suggest that the extended eastern migration route minimizes exposure to cod predation, and that resent warming conditions north of Iceland may result in a northward shift in migrations and spawning locations, as occurred in the 1920s and 1930s.

Key words: capelin, *Mallotus villosus*, migration route, spawning, temperature, bathymetry, Atlantic cod, predation.

3.2 Introduction

Capelin (*Mallotus villosus*) is a small semelparous schooling smelt (family *Osmeridae*) with circumpolar distribution in the northern oceans (Vilhjálmsson, 1994). The three largest stock complexes inhabit the Barents Sea (Gjøsæter, 1998), the continental shelf off Newfoundland and Labrador including the Gulf of St. Lawrence (Templeman, 1948) and the area between Iceland, Greenland and Jan Mayen, here after called the Icelandic stock (Vilhjálmsson, 1994, 2002).

Capelin inhabit boreal ecosystems straddling the border between cold Arctic waters and temperate Atlantic/Pacific waters, and thus experiencing dynamic oceanographic conditions. Capelin most often occupy temperatures ranging from -1 to 6 °C (overall range -1.5 to 14 °C), with spawning typically occurring in warmer waters (Templeman, 1948; Vilhjálmsson, 1994; Gjøsæter, 1998). Boreal ecosystems are typically species poor with a few dominant species and strong interactions through predation (Hamre, 1994; Anderson and Piatt, 1999; Carscadden *et al.,* 2001; Astthorsson *et al.,* 2007). Capelin is the dominant pelagic forage fish and a keystone species in the boreal food web (Vilhjálmsson, 1994, 2002; Lilliendahl and Solmundsson, 1997; Carscadden *et al.,* 2001, 2002; Dolgov, 2002). In these ecosystems, the distributions, migrations and vital rates of many predator species may depend not only on the abundance but on the distribution and migration routes of the capelin. These predators include fishes, in particular the Atlantic cod (*Gadus morhua)* (Rose, 1993; Nakken, 1994; Vilhjálmsson, 2002; Hylen *et al.*, 2008), whales (*Megaptera novaeangliae, Balaenoptera acutorostrata* and *B. physalus*) (Piatt and Methven, 1992) and seabirds (*Uria aalge*),

whose colonies are often typically found where capelin concentrate (Davoren *et al.*, 2003).

Ocean climate variations are known to influence capelin distribution and migrations (Rose, 2005). Historical distribution shifts are well documented in Icelandic waters (Saemundsson, 1934) as they are on a smaller scale in the Barents Sea (Ozhigin and Luka, 1985; Gjøsæter, 1998). Recently, capelin in Newfoundland and Labrador waters have undertaken marked shifts in distribution and migration (Frank *et al.*, 1996; Carscadden *et al.*, 2001), with effects on several dependent predators (Rose and O'Driscoll, 2002; Dempson *et al.* 2002; Davoren *et al.*, 2003).

All capelin stocks migrate between spawning, juvenile, feeding and over-wintering grounds with only maturing fish participating in the feeding and spawning migration (Vilhjálmsson, 1994). The majority of capelin die after spawning when three to five years old, thus limiting transfer of migration route knowledge between generations (Templeman, 1948; Vilhjálmsson, 1994; Gjøsæter, 1998).

Despite the importance of capelin migration to fisheries and a myriad of predators, the factors that influence their migration routes from summer feeding and over-wintering grounds to springtime spawning areas remain largely unknown. In the Barents Sea and in Newfoundland and Labrador waters, capelin migration is thought to be restricted to relatively shallow areas (<500m) of the continental shelves (Gjøsæter, 1998; Mowbray, 2002). In Icelandic waters, however, maturing capelin feed during summer well to the north and west of the Icelandic continental shelf in the cold deep waters of the Iceland Sea (67 – 72 °N, 1 - 3 °C), thereafter conducting an extended spawning migration in January and February (>500 km) to the warmer coastal waters (<100 m; 5 - 7 °C) south

and west of Iceland (63 - 65 °N), where spawning occurs in March and April (Vilhjálmsson, 1994). In some years, another much smaller migration occurs later in the season (Vilhjálmsson, 1994). The typical route follows the prevailing current to the east of Iceland and follows the outer shelf edge to the spawning area south of Iceland, although in exceptional instances some capelin migrate counter to the current in a much shorter route along the west coast (Vilhjálmsson, 1994).

The putatively dominant eastern migration route is neither direct nor the shortest available, taking the fish on an extended journey well off the shelf and over deep water for over 500 km until they reach approximately 65 °N (Vilhjálmsson, 1994). As migration over such long distances is energetically costly, especially to a small fish such as capelin, we hypothesized that other factor than an assumed sense of a southern heading must be influencing the migration route, with some survival benefit outweighing the additional energetic costs of an extended migration. Various candidate factors that might influence migration routes in pelagic fish species include passive drift (McCleave, 1993), sea temperature (Ozhigin and Luka, 1985), stock size (Dragesund *et al.*, 1997), predator distribution (Mowbray, 2002; McQuinn, 2009) and bottom depth (Makris *et al.*, 2009).

The purpose of this paper is to examine the spawning migration routes of Icelandic capelin based on acoustic surveys conducted since the late 1970s (Vilhjálmsson, 1994), and to assess several hypotheses that might explain the routes taken. I begin by testing a base hypothesis that maturing capelin are simply migrating passively in the current, with ground velocity equivalent to mean current velocity. Next, I examine a bathymetry hypothesis that the routes actively follow a consistent depth contour. Then I assess two hypotheses with respect to temperature, namely that capelin

migration routes are determined by an active avoidance of unfavorably cold temperatures or by active movement following a gradient of increasing temperature, and a hypothesis that stock size influences the migration route. Finally, I develop a hypothesis that avoidance of gadoid predators that concentrate on the continental shelf leads to higher survival, which outweighs the higher energetic costs of a longer route to the spawning grounds.

3.3 Materials and methods

3.3.1 Study region

Oceanographic conditions around Iceland are strongly influenced by bottom topography. The island lies on the Greenland-Iceland-Faroe ridge which separates cold Arctic waters (<0 – 3 °C) from the warmer Atlantic waters (5 – 9 °C) to the south (Fig. 3.1) (Blindheim and Østerhus, 2005). There are strong vertical and horizontal oceanographic fronts where these waters masses meet (Malmberg *et al.,* 1996; Perkins *et al.,* 1998; Jónsson and Valdimarsson, 2005). The Greenland-Iceland ridge is located north (66 °N) of the Iceland-Faroe ridge (64 °N) causing the west coast of Iceland to have warmer waters than the east coast.

The cold waters north of Iceland in which capelin feed and over-winter are dominated by two distinct currents; the East Greenland Current (Polar water of < 0 °C) and the East Iceland Current (Arctic water of 1 – 3 °C) (Malmberg *et al.,* 1996). The East Greenland Current flows south along the east coast of Greenland in the opposite direction to the warm North Icelandic Irminger Current that flows north along the west coast of

Iceland. The flow of the North Icelandic Irminger Current is highly variable among years causing variable hydrographic conditions on the shelf north of Iceland (Malmberg *et al.*, 1996; Jónsson and Valdimarsson, 2005). The somewhat warmer East Icelandic Current follows the shelf edge north of Iceland clockwise around the east coast until it meets the warm Atlantic waters southeast off Iceland, there forming the Iceland-Faroe front (Perkins *et al.*, 1998). As the warm and cold currents meet both turn east and flow along the ridge towards the Faroe Islands. The Iceland-Faroe front has strong temperature gradients and currents that vary in direction and velocity (2 – 65 cm s^{-1}) with depth (Perkins *et al.*, 1998).

The East Iceland current is baroclinic in the surface to 200 m, and flows southeast along the shelf slope at the speed of 3 – 8 cm s^{-1} in winter (Jónsson, 2007). Below 200m, the current is slower and barotropic, with variable directions. Offshore from the shelf slope the current has the same southeast direction but is barotropic and slower flowing (Jónsson, 2007).

For the present analyses, data from the east and west migration routes were inferred to bifurcate at 19.5 °W and analysed separately as a consequence of the different latitude of oceanographic fronts along the north-to-south migration axes. Oceanographic conditions around Iceland are measured on standard transects four times annually in February, May, August and November (Anon, 2009a). We estimated the annual winter condition on the shelf north of Iceland by calculating the average temperature in the surface 200 m on the Siglunes hydrographic section, stations 1 to 5, (18.83 °W; 66.26 – 67.00 °N; Fig. 3.1) (Ólafsson, 1985, 1999).

3.3.2 Acoustic data

Data on abundance and distribution of maturing capelin were available from the winter (January – March) acoustic assessment surveys of the Marine Research Institute, Reykjavik, Iceland that began in the late 1970s (Vilhjálmsson, 1994). The survey region is the northwest, north and northeast of Iceland (63 – 68 °N and 8 – 28 °W). These surveys use a 2-stage adaptive design in which both survey grid and boundaries are modified during the survey depending on capelin distribution and weather. A pilot survey typically covers the whole shelf edge of the study region using parallel or zigzag transects spaced 15-20 nautical miles apart. Transects run perpendicular to the shelf edge from the shelf break seaward over deeper waters. When the capelin migration is located, the distance between transects is reduced to 5 – 10 nautical miles. For a detailed description of the surveys see Vilhjálmsson (1994) and Vilhjálmsson and Carscadden (2002).

In the present study, digitized acoustic data were available from 33 winter surveys conducted by three research vessels over the 16 year period from 1992 – 2007 (Appendix 3.1). No surveys were conducted in 1994, 1996 and 1997. All digital data were recorded from Simrad EK500 echosounders with hull mounted 38 kHz split-beam transducers (Simrad ES38B: 7°, 3 dB beam, pulse length 1 ms, receiving bandwidth 3.8 kHz and ping rate variable from 0.5 – 1 ping s^{-1}). Data were stored digitally in 1 m vertical bins. Survey speed was 10 nautical miles h^{-1} over 24 hours. The echosounders were calibrated prior to each survey according to Foote *et al.* (1987). Backscatter was recorded to 500 m depth and echosounder detected bottom was recorded separately. For all data a near field range of ten meters from the transducer was eliminated and depth was corrected for the draft of the transducer.

Biological sampling was conducted using a pelagic trawl with 9 – 42 mm mesh in the cod end. For each fishing set, 100 haphazard selected capelin were measured for length, weight, sex, maturity, gonad weight and age. Capelin were considered to be maturing in that year if gonads were developing by January 1st (Vilhjálmsson, 1994). Fishing frequency varied from < 1 set day^{-1} during pilot surveying to 8 sets day^{-1} once the capelin migration had been located. Fishing was conducted to cover backscatter changes in density, location in the water column or general appearance and shape of the acoustic marks.

Echograms were edited using Echoview®v.4.8 (Myriax, Hobart, Tasmania, Australia). Noise signals attributed to bad weather or trawling activities were eliminated. Bottom depth on echograms was defined by using the echosounder detected bottom smoothed by the median of five adjacent values to reduce roughness from vessel pitch and roll. Depths were corrected for the different transducer placements on the vessels used during the years of this study. Backscatter judged to be from capelin was assigned biological information from the nearest fishing set. Capelin were typically well isolated from other species in the acoustic data. Catches from backscatter judged to be capelin were virtually 100 % capelin in all cases with the exception of one 12 h period during a single survey when capelin were mixed with herring - these data were not used in the analyses. All data were integrated to give backscatter area estimates (S_a) in 5 m surface-referenced layers for each 100 m of survey track, with total backscatter the sum of the vertical bins within each horizontal bin. The spawning migration, in some years, temporarily overlapped with the distribution of over-wintering juveniles on the shelf or shelf edge northwest, north and northeast of Iceland causing mixing of the immature and

the mature part of the stock. As the present study addressed migration of the mature part of the stock, bins having > 50 % juvenile capelin were not used in these analyses. For consistency with previous analyses, S_a values of maturing capelin were converted into number of fish per 100 m of survey track using the target strength equation used in the Icelandic surveys:

TS (dB) = 19.1 * log (L) – 74.5 dB, L = length of fish (cm) (Vilhjálmsson, 1994).

Acoustic backscatter was allocated to the west (counter-clockwise around Iceland) or east (clockwise) migration route based on location. No mature capelin were located between longitudes 19.25 – 21.72 °W north of Iceland and this gap was used to separate the east and west migration routes. Hence, the east migration included all capelin located east of longitude 19.25 °W along the north coast, then clockwise around the east coast to 18.75 °W off the south coast. The west migration included all capelin located west of 21.72 °W and north of 65.50 °N. Historically the eastern migration route is the dominant spawning route (Vilhjálmsson, 1994). The western migration route is located on important cod fishing grounds where commercial vessels monitor capelin presence and scientific surveys are conduced after capelin presence is reported by commercial vessels. Capelin south of 65.50 °N and west of 18.75 °W were eliminated from the analysis as it was unclear which route was being taken.

Migration ground speed was calculated in years in which repeated surveying had been conducted along the eastern migration route. For sequential surveys spanning the full range of the migrating shoals, centroids of distribution were calculated as the mean

position weighted by capelin density. Migration velocity was estimated as distance and direction travelled based on the straight line distance between centroids, divided by the difference in median time between surveys. Migration velocity was then compared to mean current velocity in that area from the literature.

3.3.3 Temperature

Sea surface temperature (SST) was assumed to be an appropriate proxy for ambient temperature within the epipelagic layer (<200 m in winter) because the thermocline was sufficiently strong between 200 – 300 m that the epipelagic layer was thought to be thermally isolated from deeper waters despite having some temperature variability within the layer itself (Fig. 3.2) (Jónsson, 2007; Jónsson and Valdimarsson, 2005; Kara *et al.,* 2003). The daily optimum interpolation SST provided by the National Oceanic and Atmospheric Administration of the United States (ftp://eclipse.ncdc.noaa.gov/pub/OI-daily-v2/NetCDF/), based on advanced very high resolution radiometer satellite data, version 2, was used as it covers the whole time period and location of interest (Reynolds and Chelton, 2010). These data have a spatial resolution of 0.25° latitude/longitude, temporal resolution of one day and represent the top 0.5 m of the ocean surface (Xue *et al.,* 2003). For detailed description of methods used to calculate SST see Reynolds *et al.* (2007). SST data were linked to capelin acoustic data by assigning a SST value to every 0.25 ° latitude/longitude bin in which capelin were present each day. SSTs inshore and offshore from the migration route were estimated by first defining the inshore and offshore boundary of the migration. The average SST of three spatial bins (total 0.75 °latitude/longitude) neighboring the boundary bins were then used to estimate

temperatures inshore and offshore of the migration route. Presumed temperatures estimated from all years excluding 1994, 1996 and 1997.

3.4 Results

3.4.1 The spawning migration

The capelin spawning migration started in deep waters north of Iceland (68 °N) in January and ended in shallow coastal waters south and west of Iceland (63.5 °N) in March and April. Two migration routes along the east and west coasts were utilized (Fig. 3.3). For all years examined from 1992-2007 except 2001, the vast majority of capelin used the eastern route (Fig. 3.4). The predominant eastern route had a north-to-south migration axis ranging from 68.00 – 63.25 °N (>500 km); the much less used western route was shorter from 67.75 – 65.50 °N (ca. 250 km). The eastern route was further extended as it skirted the shelf edge and did not cross the shelf until south of 65 ° N (Fig. 3.3). Use of the western route tended to occur in late February – early March, later than the dominant eastern route migrations.

Juvenile capelin were found on both migration routes but were more numerous on the western (68 %) than the eastern route (2 %) (Fig. 3.5a, b), and were most commonly located west of 19.25 °W and north of 66 °N. On the eastern route, the frequency of juveniles declined to the south with no juvenile abundance >50 % south of 64.75 °N.

The weighted (by fish density) average vertical depth of capelin in each 100 m by 5 m depth bin further binned into 0.25 °latitude/longitude bins to match the SST data, ranged from 15 to 433 m (Fig. 3.6a, b). Average depths differed between routes (western

109m, eastern 130m, $t = 3.09$, $p = 0.002$, $df = 1797$). Average depth did not change with latitude on the eastern route ($F_{[1,1679]} = 3.52$, $p = 0.061$) but decreased with a more southern location on the western route ($F_{[1,116]} = 8.96$, $p = 0.003$). Ninety-nine and 79% of capelin using the eastern and westerns routes, respectively, occurred in the epipelagic layer at depths < 200 m, thereby supporting the use of SST as the ambient temperature of the spawning migration.

3.4.2 Active or passive migration?

Capelin using the eastern route migrated at an average depth of 125 m within the flow of the dominant surface East Iceland Current. The average flow at 125 m depth declined from a maximum of 5 cm s^{-1} (4.3 km day^{-1}) over the slope to 0 cm s^{-1}, 60 km further offshore (Jónsson, 2007). Migration ground speed for the eastern route ranged from 2.2 – 27 km day^{-1} (Table 3.1). In all cases but one migration speed exceeded the maximum current flow of 4.3 km day^{-1}. Migration speeds could not be calculated for the western route.

3.4.3 Bathymetry

Bottom depth along the migration route ranged from 24 to 1688 m (Fig. 3.7a, b) and declined with a more southern location (eastern route: $F_{1,1679} = 1270.7$, $p < 0.001$, $R^2 = 0.43$; western route $F_{1,116} = 70.5$, $p < 0.001$, $R^2 = 0.38$). On the dominant eastern route capelin tended to follow the shelf break but stayed over deep water off the shelf until they were south of 65 °N (Fig. 3.3). The continental shelf is defined here by the 200 m isobath. The shelf break is at its steepest northeast of Iceland (Fig. 3.1) causing large variance in

bottom depth within latitude bin, maximum 1400 m at 67.1 °N. The variance decreased with a gentler shelf break to the south.

On the western route, in contrast to the eastern route, capelin moved onto the shelf as far north as 66.5 °N. The migration followed the shelf break in some years (2001; Fig. 3.3) but crossed onto the shelf in others (2005). The shallower bottom depths encountered on the western route reflect the bathymetry of the area.

3.4.4 Temperature

The ambient temperature of the capelin migration ranged from -0.1 to 8.2 °C (Fig. 3.8a, b). On the eastern route, the mean ambient temperature of the migration was constant at about 2.5 °C as capelin migrated southward until they reached about 65.50 °N. Further south there were rapid and continuous temperature elevations to > 7.5 °C, with all increases within latitudinal ranges of 0.5 °N significant except the final one furthest south (Fig. 3.9a). For the western route, the mean temperature fluctuated between 2 and 5 °C but did not increase with a more southern location, except between 65.75 – 66.25 °N and 67.25 – 67.75 °N (Fig. 3.9b).

A temperature corridor appeared to act as a funnel to guide capelin southward on the eastern route. The mean temperatures inshore of the eastern route were approximately 1 °C warmer than the mean migration temperature north of 65 °N but further south the difference diminished to < 0.5 °C (Fig. 3.10a). Offshore from the migration route the mean temperature was about 1 °C lower than within the route north of 67 °N but this difference also decreased as the migration moved south. In contrast to the temperature corridor suggested for the eastern route, the mean temperatures inshore and offshore for

the western route fluctuated above and below the mean migration temperature with no southward trend and a maximum difference of 1.5 °C (Fig. 3.10b).

On the eastern migration route, as capelin approached the Iceland-Faroes front, rapidly increasing temperatures coincided with abrupt changes in the heading of the migration (Fig. 3.11). North of 65 °N, with temperatures < 2.6 °C, capelin rarely ventured onto the shelf, but south of 65 °N (Fig. 3.12a), temperatures increased sharply to 6.4 °C, and within <100 km an average of 50 % of capelin had crossed onto the shelf. Within a further 50 km (at 63.5 °N), temperatures reached a maximum of 7.9 °C and 81 % of capelin had turned west and onto the shelf. This pattern varied little among years, with all cohorts from 1992 to 2007 crossing the shelf between 65 and 63.5 °N (Fig. 3.12a). For the western route, movement of capelin onto the shelf also coincided with increasing temperatures off the shelf but the temperature change was much more limited, from 4.1 to 4.8 °C (Fig. 3.12b).

3.4.5 Spawning stock size

There was no relationship between stock size and the migration route taken during the years of this study, with the eastern route dominating over a range of stock sizes from <700,000 t to >1,800,000 t (Fig. 3.4).

3.5 Discussion

The spawning migration of the Icelandic capelin stock appears to follow two basic routes from the northern feeding region to the south and west coast spawning areas. The primary

route follows the edge of the continental shelf to the east of Iceland until the warm waters of the Iceland-Faroes front are encountered. South of 65 °N the route abruptly veers to the west and onto the shelf (< 200 m bottom depth) between latitudes 65 to 64 °N. At these latitudes, the capelin encountered the warm waters of the Iceland-Faroe front (Blindheim and Østerhus, 2005). A secondary route exists to the west of Iceland but this route is not often used.

The dominant migration route tracks the north to south flows of the East Iceland Current. The velocity of the migration greatly exceeded that of the mean current, however, indicating that this is an active and not a passive migration. The mechanisms that cue the start of the migration and inspire capelin to seek their spawning grounds to the south are beyond the scope of this study, but they are apparently innate as each cohort makes a single migration thus eliminating any opportunity for learning or social transmission. The annual light cycle (very little at these latitudes in January when the migration begins) could be a cue but would not explain why capelin head south or how they know which way south is. These mechanisms await further investigation.

The migration did not follow a specific depth contour but followed the shelf edge until south of 65 °N when the migration route suddenly veered to the west and onto the shelf (< 200 m bottom depth). This pattern was displayed by every migration cohort studied, from 1992 to 2007 (excluding 1994, 1996 and 1997), with the migration entering the shelf at the same latitude (64 - 65 °N) each year. This migration pattern can neither be explained by a gradient of increasing temperature along the north-to-south migration range (Fig. 3.9a) nor by unfavorable temperatures onshore and offshore from the migration, although a thermal corridor is suggested (Fig. 3.10a). Interestingly, migration

onto the shelf coincided with increasing ambient temperatures (Fig. 3.12a) associated with warm Atlantic waters (Blindheim and Østerhus, 2005). In all years examined, migrating capelin did not move onto the shelf until after encountering warm Atlantic waters.

The eastern route was used not only in the years from 1992 to 2007 (excluding 1994, 1996 and 1997) studied in the current studie but evidence exists that this route was also used during the previous decade. Vilhjálmsson (1994) reported a similar route and the same latitude of on shelf movement for the 1979 to 1991 cohorts (Appendix 1: Descriptions of surveys of stock distribution and abundance). The 2008 – 2010 cohorts apparently have followed the same route (Anon, 2008; Anon, 2009b; Anon, 2010). Hence, we conclude that for at least three decades every capelin spawning cohort except that of 2001 has followed the same primary spawning migration route. During this period, spawning stock size has varied more than an order of magnitude, from 171 to 1881 thousand tons (Anon 2010; Fig. 3.4) without affecting the migration route, thus offering no support for the density-dependent stock size hypothesis.

That the migration route showed little evidence of a north-south gradient in temperature was inconsistent with the hypothesis that capelin follow a gradient of increasing temperature. There is evidence, however, that the route follows a funnel of favored temperature (ca. 2.5 °C) that entrains the fish between the warmer coastal waters and cooler offshore waters. This pattern weakens as the fish travel southward. It is also noteworthy that the temperature differences both toward the continental shelf and to the offshore are small (typically +-1 °C) and well within the range of temperatures where capelin are commonly located (Rose, 2005). Hence, it does not appear that any

temperature barriers exist. More likely the southward flowing current and thermal funnel entrain the southward migration until a threshold of increasing temperatures is reached at the Iceland-Faroe front, at which point the maturing fish divert westward onto the shelf and towards the coastal spawning region.

Spawning migration routes evolve as fish use movement to maximize reproduction (Jørgensen *et al.*, 2008) and to avoid unfavorable environments (Harden-Jones, 1968). The capelin spawning migration ultimately reaches a shallower (< 100 m) and warmer environment (5 – 7°C) than they occupy during the summer feeding and over-wintering period (> 500 m and 1 – 3°C; Vilhjálmsson, 1994), where there is suitable spawning habitat. The shortest migration route to these grounds would cross the continental shelf to the east or west of Iceland. To the east such a route would follow prevailing currents, as does the actual indirect eastern route, without encountering temperatures outside their normal range. That this route is never taken suggests that the extended eastern route has a survival advantage beyond simple entrainment that outweighs the extra costs of a longer migration. The Icelandic continental shelf is home to a large cod stock which is the main predator of the capelin (Vilhjálmsson, 2002) (Fig. 3.13). Cod distribution is limited to the 500 m depth contour with the bulk of the stock found shallower than 200 m (Begg and Marteinsdottir 2002; Anon, 2010). It is possible that predation from gadoids, in particular Atlantic cod, has led to the evolution of a longer migration route that leads to higher survival in spawning capelin. In short, capelin avoid crossing cod ground until it absolutely necessary. In other ecosystems of the north Atlantic, cod are known to influence capelin distribution at small and large scales (Rose and Leggett, 1990; Rose, 1993; Mowbray, 2002; McQuinn, 2009). It is of further interest

that as in other cod-capelin ecosystems, cod distribution appears to be linked to the pattern of the capelin migration (Rose, 1993). In Icelandic waters, cod abundance is known to be consistently higher where capelin move onto shelf between 64 °N and 65 °N than north of 65 °N (Begg and Marteinsdottir 2002; Anon, 2010), suggestive of a counter-move by cod in the predator-prey arms race (Dawkins and Krebs, 1979). The capelin strategy, nonetheless, appears to limit the exposure to predation by cod as much as possible in order to reach their spawning grounds on the south coast.

3.5.1 The western spawning migration route

For the 13 cohorts studied only a small fraction of capelin (1%) used the western spawning migration route. The influences of temperature and bathymetry were not evident on the western route as capelin moved onto the shelf with a more southern location regardless of limited changes in temperatures (Fig. 3.9b). In addition, migration temperatures were highly variable within latitude bins and did not gradually increase with a more southern location (Fig. 3.8b). The west coast is dominated by the unfavorably cold East Greenland Current (< 0 °C) flowing south and the warm North Icelandic Irminger Current flowing north with a strong oceanographic front where the currents meet (Malmberg *et al.*, 1996; Jónsson and Valdimarsson, 2005). Temperatures in the region range from -1.8 to 7.5 °C (measured at 80 m depth; Fig. 6 in Jónsson and Valdimarsson, 2005). The variable and unstable temperature regime may have restricted the evolution of a consistent off shelf then on shelf migration route. In comparison, the east coast has limited temperature variability as the East Iceland Current (1 - 3 °C) flows east then south

along the shelf edge parallel to the slightly warmer coastal current (Jónsson, 2007), and here no oceanographic front is present until south of 64 – 65 °N (Perkins *et al.*, 1998).

There is no unequivocal explanation for why the majority of the 2001 cohort took the little used western route. It is possible that atypical distributions of the maturing capelin stock in fall or early winter led to the use of the western route. Another possibility is that unusually stable and warm oceanographic conditions north of Iceland led to capelin following the shelf edge without encountering unfavorably cold waters. These questions cannot be answered with the present data. Whatever the reason for the use of the western route in 2001, the cohort produced in that year was above average at recruitment to the spawning stock three years later (Fig. 3.4; Anon, 2010).

In summary, I believe that the spawning migrations of the Icelandic capelin are an innate response that provokes maturing fish to travel south in search of spawning habitat having temperatures in the around of 5 °C. Capelin begin their spawning migration when they are located north of 67 °N where hydrographic conditions are influenced by the East Greenland Current (< 0 °C) west of 20 °W and by the East Iceland Current (1 – 3 °C) east of 20 °W (Blindheim and Østerhus, 2005). I believe that the persistence of the cold East Greenland Current compels most capelin to divert to the eastern route, and has provided relatively stable guideposts that capelin have used to develop a consistent migration route. Capelin appear to follow a relatively narrow thermal funnel but at the same time avoid any cross-shelf mo, Icelandic capelin is the only capelin stock that can actively choose between two different migration routes to the same spawning ground. The two routes vary in more ways than having different temperature regimes. The western route is upstream where as the eastern one is downstream and three times longer. On the western

route the capelin are likely to encounter dense concentrations of predatory cod as far north as 67 °N (Anon, 2010; Begg and Marteinsdottir, 2002) at the very onset of the migration whereas on the eastern route cod can be avoided until the last part of the migration across the continental shelf. How these factors influence the migration route selection of the capelin is a compelling question and worthy of future research.

3.5.2 The future: shift in capelin spawning ground and migration route?

Capelin shifted their distribution northward during a warm period in the 1920s and 1930s in Icelandic waters, abandoning their south coast spawning areas in favor of alternative grounds on the north coast (Saemundsson, 1934). In the 1920s and 1930s, winter sea temperatures north of Iceland increased to 4 – 5 °C from 0 – 1 °C on the northeast corner of the northern shelf (66.29 °N and 15.31 °W; Saemundsson, 1934), and the entire northern shelf was likely dominated by warm Atlantic waters creating oceanographic conditions similar to the ones found on the south coast of Iceland today. During this warm period the main spawning areas for the capelin shifted from the south to the north coast of Iceland. Factors other than temperature are known to influence capelin spawning locations, in particular substrate type (Carscadden *et al.*, 1989; Nakashima and Taggart, 2002) and water circulation (Thors, 1981). I assume that suitable physical habitat is a prerequisite for spawning. There is limited information available on the marine habitat on the shelf north of Iceland, nevertheless, that capelin successfully spawned there several years in a row during the warm 1920s indicates such habitat occurs there. The weight of this evidence suggests that no critical adverse environmental factors preclude capelin spawning north of Iceland other than temperature, and that if temperatures to the north of

Iceland exceed a threshold of 5 °C in January or February (Saemundsson, 1934), capelin are likely to spawn there.

In the two decades from the 1980s until 2000 there was no indication of warming on the northern shelf or a shift in capelin migration or spawning grounds, with only minor variation in feeding migrations (Vilhjálmsson, 1994, 2002). Since 2000, however, the distribution of immature capelin and maturing fish in fall has gradually been moving north, causing a reduction of capelin on the Iceland shelf (Astthorsson *et al.,* 2007) and a prolonged spawning migration to the spawning grounds south and west of Iceland (Vilhjálmsson, 2002). Since 1990, winter temperatures on the shelf north of Iceland show large inter-annual variability, from 1 °C in 1995 to 4 °C in 2008, with an increasing trend since 1998 (Fig. 3.14) that coincides with the northward extension of the feeding range. My results suggest that winter temperatures on the shelf north of Iceland would have to increase by a few more degrees before capelin spawning grounds are likely to shift to the north coast. In particular, according to the present analyses, cross-shelf migration was triggered when temperatures exceeded 4.5 °C, with capelin spawning at 5 – 7 °C (Vilhjálmsson, 1994). Hence, if winter temperatures north of Iceland reach 5 – 7 °C, an additional increase of 1 – 3 °C, it is predicted that the spawning grounds will shift to the north of Iceland, as they did in the 1920s.

As a final comment, it is important to note that warmer temperatures north of Iceland are thought not to be caused by local warming but by increased flow of the warm North Iceland Irminger Current onto the shelf (Jónsson and Valdimarsson, 2005). The flow of this current is difficult to predict as it is characterized by large seasonal and inter-annual variability (Jónsson and Valdimarsson, 2005). Nonetheless, decadal shifts have

been recorded, as evident in the 1920s and 1930s, with large flows of Atlantic Ocean waters onto the shelf raising local water temperatures by as much as 5 °C (Saemundsson, 1934). Future predictions of capelin migrations and spawning hence depend for the most part on the variable oceanographic conditions on the shelf north of Iceland, with these further complicated by effects of larger scale climate change. Although the trend appears to be towards general warming in these high latitudes, some models predict temperatures north of Iceland to decrease by 0.5 °C during the next two decades, relative to 2000, as a consequence of the melting of the Arctic ice cap (Furevik *et al.*, 2002). Constant monitoring of oceanographic conditions and the locations of the capelin are likely to be the only way to make short term predictions of their likely spawning areas and migrations.

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3.8 Tables

Table 3.1. Ground speed of capelin migrating on the eastern route in the East Iceland Current.

Year	Migration centeroid	Median date	Ground speed (km day^{-1})
2003	66.51 ° N – 11.63 °W	9 Jan. 07:10 am	7.3
	66.24 ° N – 11.05 °W	14 Jan. 08:45 pm	
	66.16 ° N – 10.87 °W	20 Jan. 10:25 am	2.2
2004	67.02 ° N – 15.30 °W	10 Jan. 00:10 am	7.7
	66.86 ° N – 13.29 °W	27 Jan. 05:12 pm	
2006	67.09 ° N – 13.35 °W	14 Jan. 22:30 pm	9.2
	66.59 ° N – 11.98 °W	23 Jan. 10:00 pm	
	65.04 ° N – 11.45 °W	30 Jan. 10:00 am	27.0
2007	66.47 ° N – 11.79 °W	25 Jan., 10:25 am	19.3
	65.76 ° N – 11.55 °W	29 Jan., 01:36 pm	

3.9 Figures

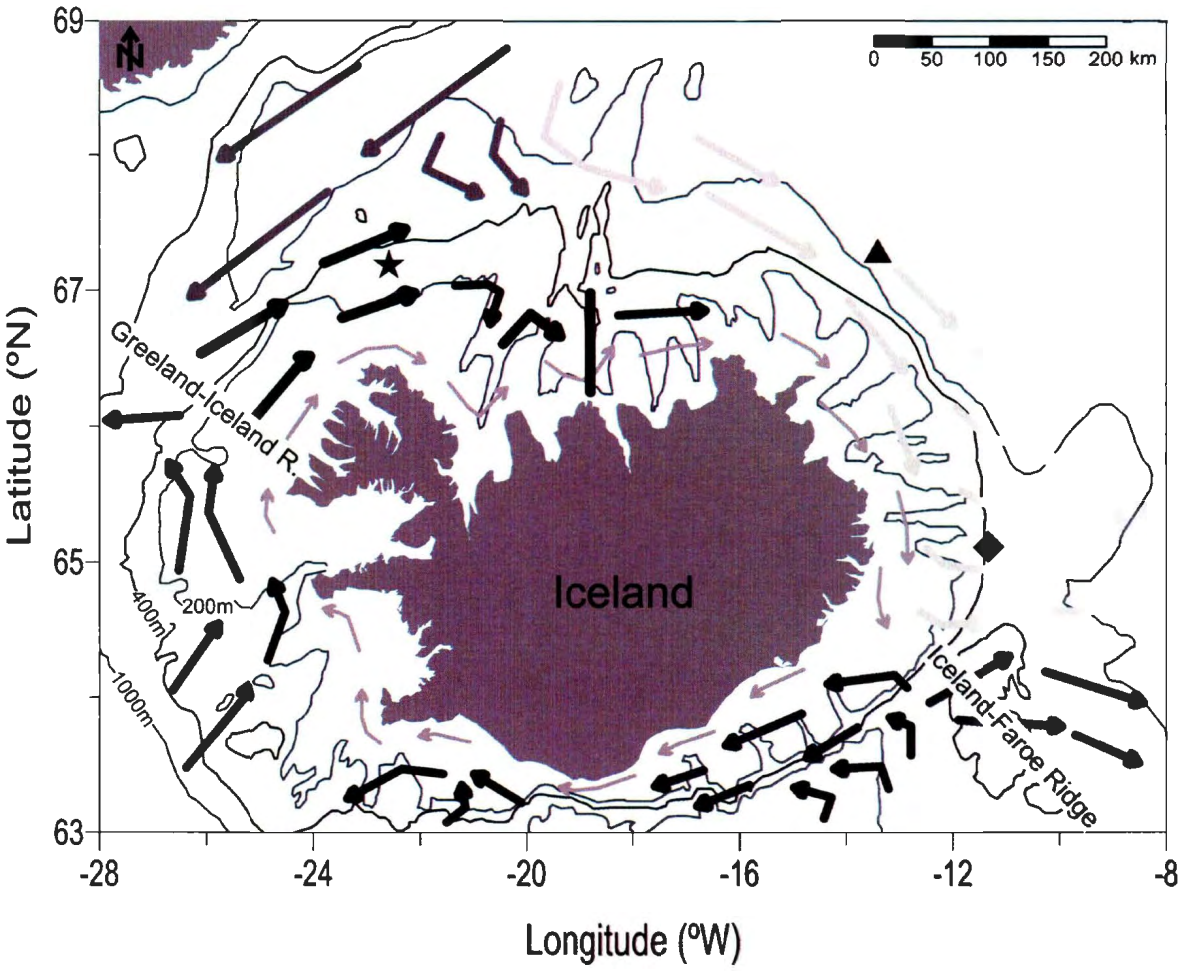

Figure 3.1. Surface currents and water masses around Iceland. Black arrows: The Irminger current (warm Atlantic water: 6-8 °C; Vilhjálmsson, 1994); light gray arrows: East Iceland Current (cold Arctic water: 1-3 °C; Vilhjálmsson, 1994); dark grey arrows: East Greenland Current (cold Polar water: < 0 °C; Vilhjálmsson, 1994); narrow gray arrows: coastal current. Redrawn from Stefánsson and Ólafsson (1991). Siglunes hydrographic section, stations 1-5, black vertical line north of Iceland. Symbols (filled triangle, diamond and star) present location of temperature profiles in Fig. 3.2.

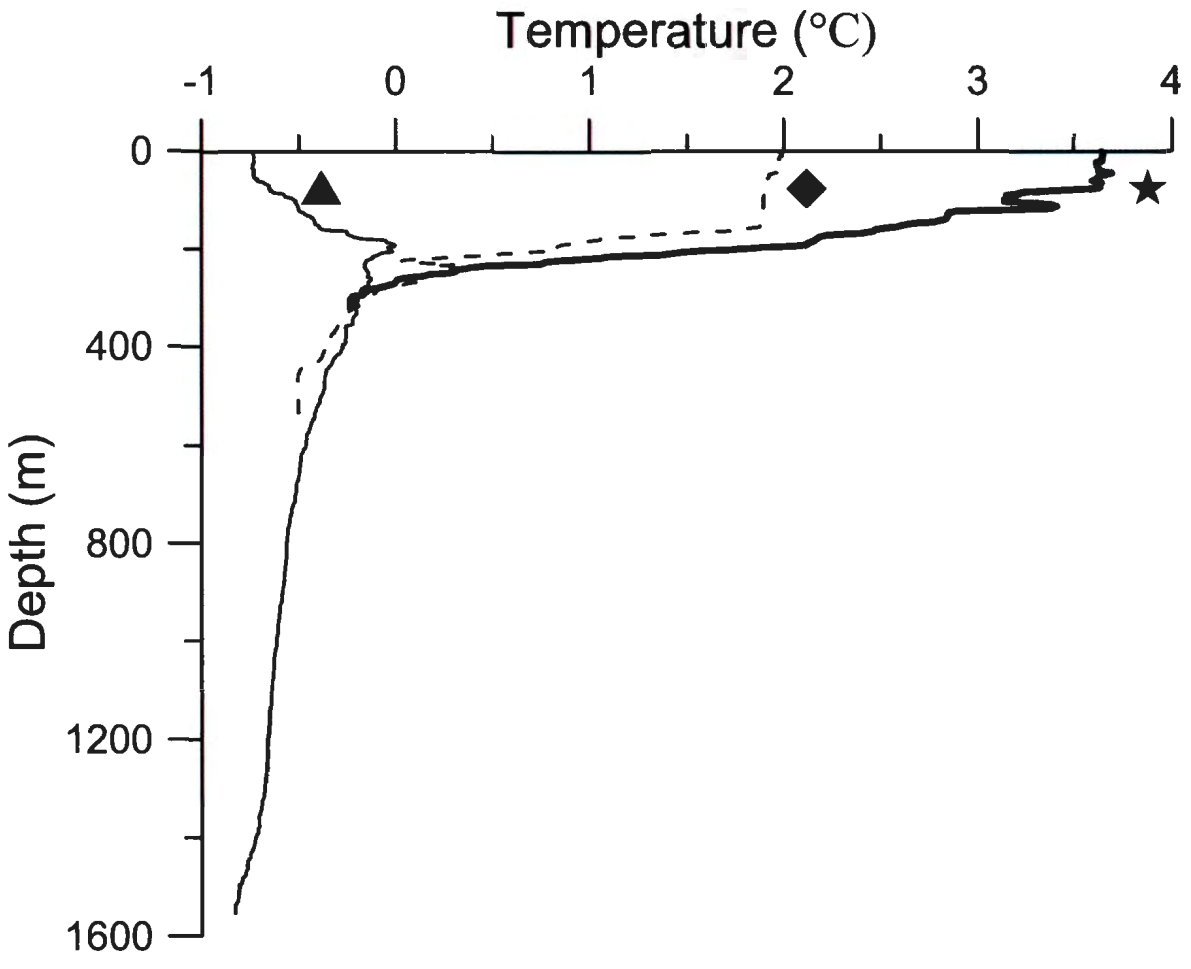

Figure 3.2. Temperature profiles, surface to bottom, from the East Iceland Current at two different locations, 67.2 °N - 13.6 °W (filled triangle; in Fig. 3.1) and 65.0 °N - 11.3 °W (filled diamond; in Fig. 3.1), and the North Icelandic Irminger Current, 67.2 °N - 22.6 °W (filled star; in Fig. 3.1). Data were collected February 19-21, 2002, for the East Iceland Current but on February 17, 1998, for the North Icelandic Irminger Current. Temperature profiles from ICES Oceanographic Database and Services (http://www.ices.dk).

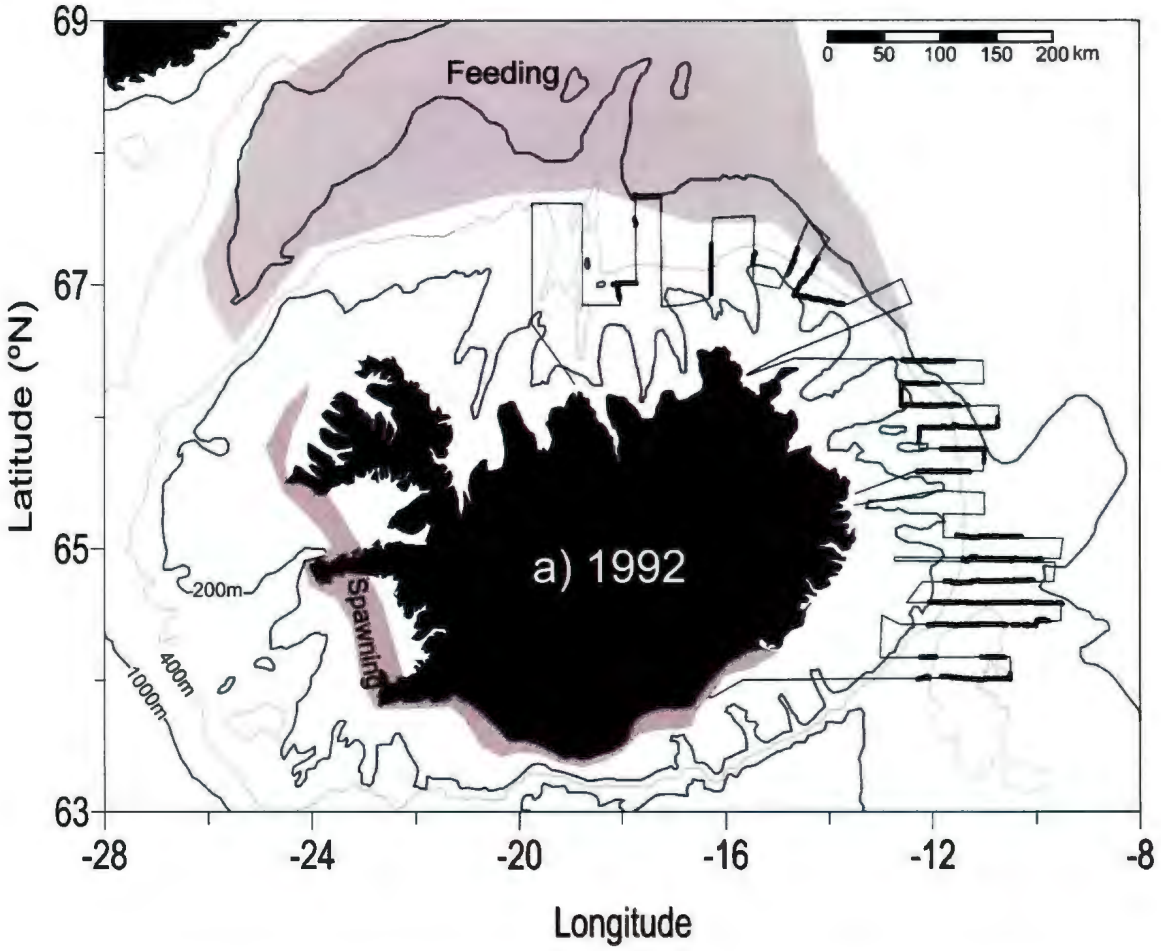

Figure 3.3a. The study region, survey tracks (narrow black line) and location of the spawning migration in January (black dots), February (red dots) and March (green dots) in Icelandic waters from 1992 to 2007. Years 1994, 1996 and 1997 are missing as no surveys were conducted. The western and eastern migration routes bifurcate at 19.25 °W north of Iceland. Spawning grounds (light grey) redrawn from Vilhjálmsson (1994). Summer feeding area (light gray) extends north to 72 °N based on Vilhjálmsson (1994) and Vilhjálmsson and Carscadden (2002). 200 m, 400 m and 1000 m depth contours displayed (gray lines).

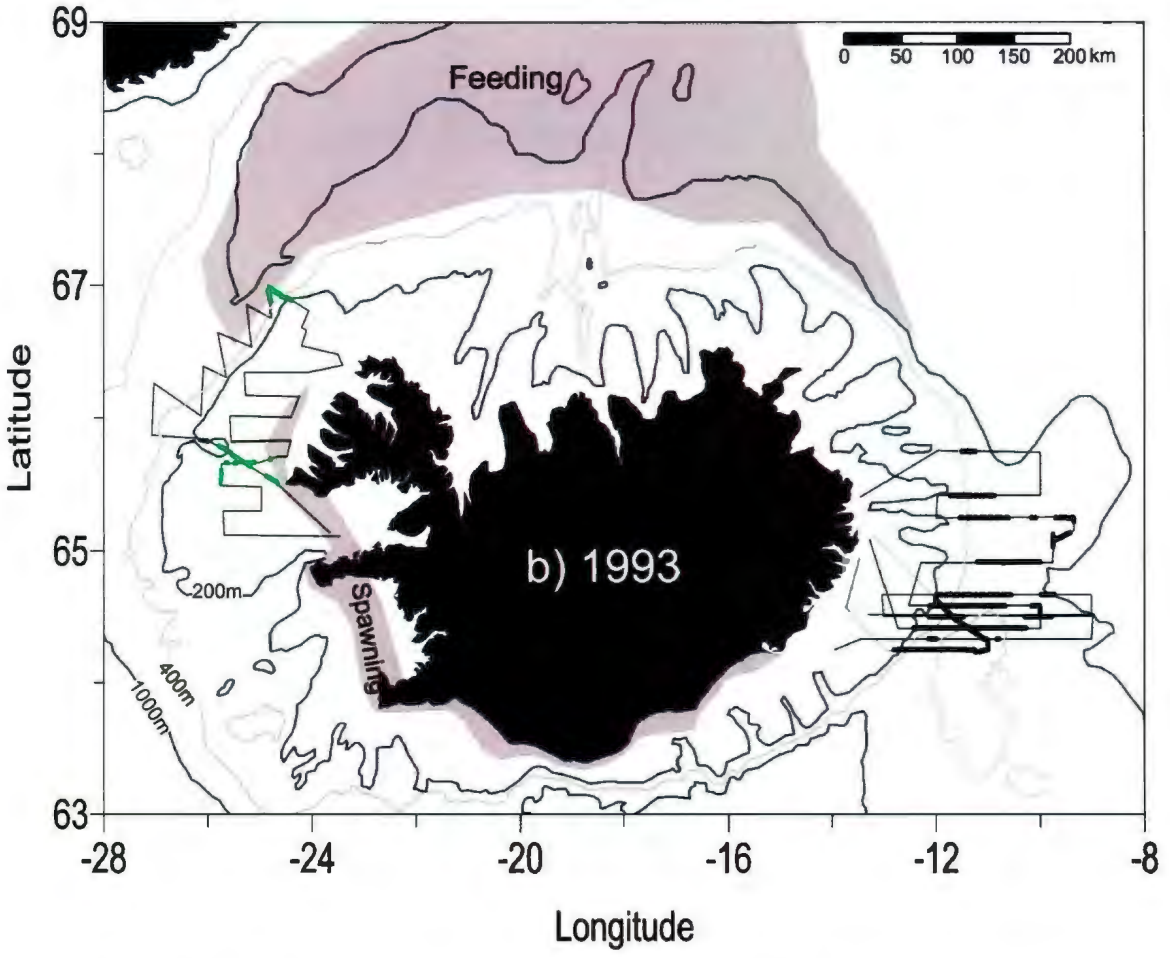

Figure 3.3b. The study region, survey tracks (narrow black line) and location of the spawning migration in January (black dots), February (red dots) and March (green dots) in Icelandic waters from 1992 to 2007. Years 1994, 1996 and 1997 are missing as no surveys were conducted. The western and eastern migration routes bifurcate at 19.25 °W north of Iceland. Spawning grounds (light grey) redrawn from Vilhjálmsson (1994). Summer feeding area (light gray) extends north to 72 °N based on Vilhjálmsson (1994) and Vilhjálmsson and Carscadden (2002). 200 m, 400 m and 1000 m depth contours displayed (gray lines).

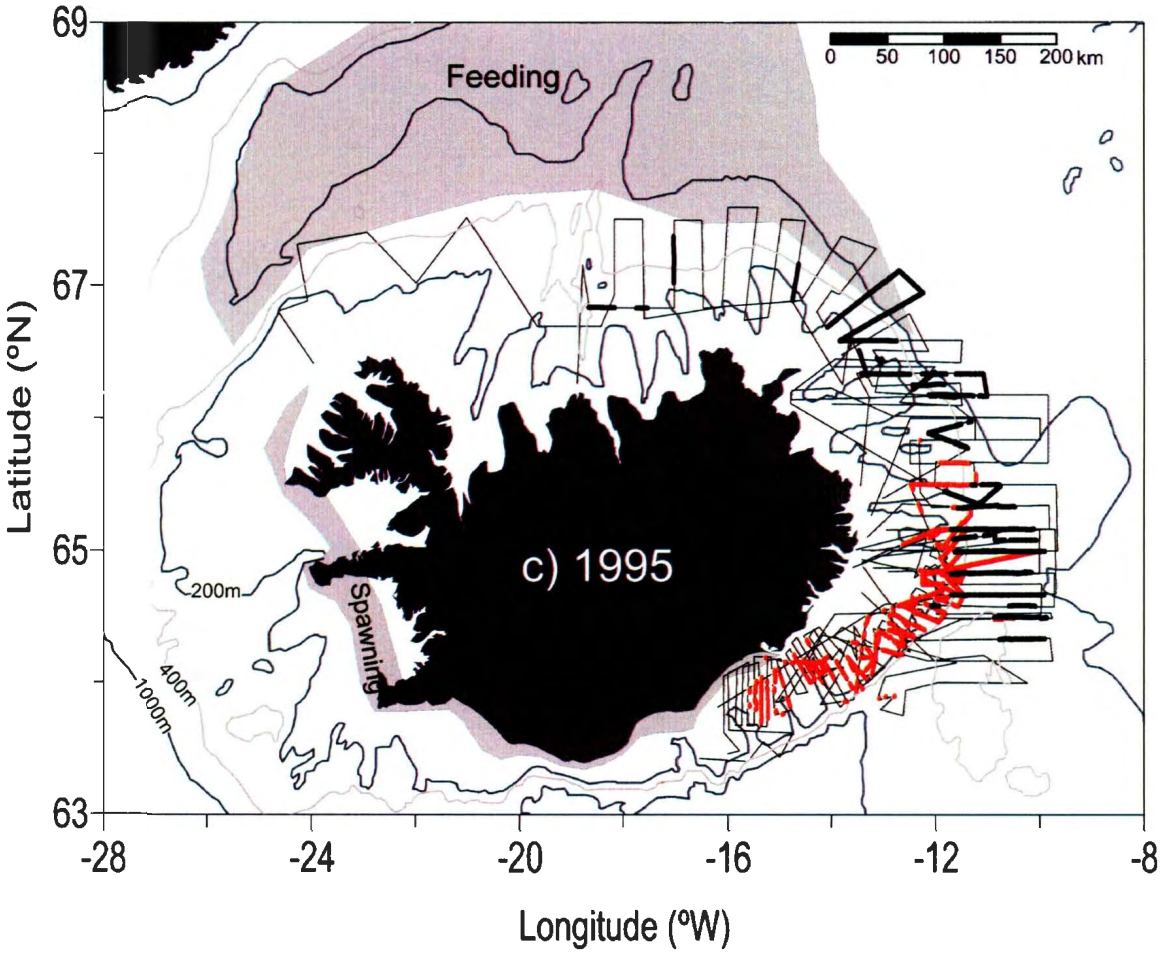

Figure 3.3c. The study region, survey tracks (narrow black line) and location of the spawning migration in January (black dots), February (red dots) and March (green dots) in Icelandic waters from 1992 to 2007. Years 1994, 1996 and 1997 are missing as no surveys were conducted. The western and eastern migration routes bifurcate at 19.25 °W north of Iceland. Spawning grounds (light grey) redrawn from Vilhjálmsson (1994). Summer feeding area (light gray) extends north to 72 °N based on Vilhjálmsson (1994) and Vilhjálmsson and Carscadden (2002). 200 m, 400 m and 1000 m depth contours displayed (gray lines).

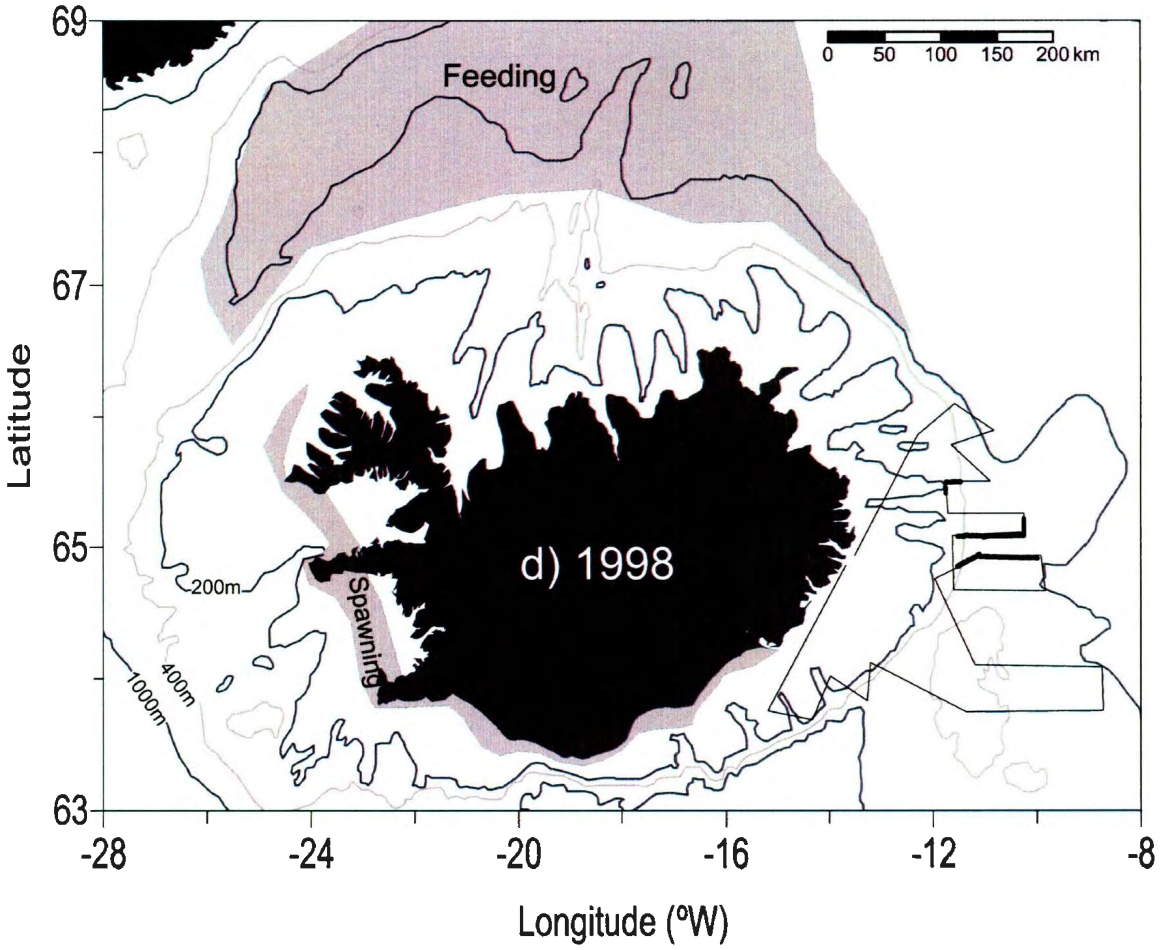

Figure 3.3d. The study region, survey tracks (narrow black line) and location of the spawning migration in January (black dots), February (red dots) and March (green dots) in Icelandic waters from 1992 to 2007. Years 1994, 1996 and 1997 are missing as no surveys were conducted. The western and eastern migration routes bifurcate at 19.25 °W north of Iceland. Spawning grounds (light grey) redrawn from Vilhjálmsson (1994). Summer feeding area (light gray) extends north to 72 °N based on Vilhjálmsson (1994) and Vilhjálmsson and Carscadden (2002). 200 m, 400 m and 1000 m depth contours displayed (gray lines).

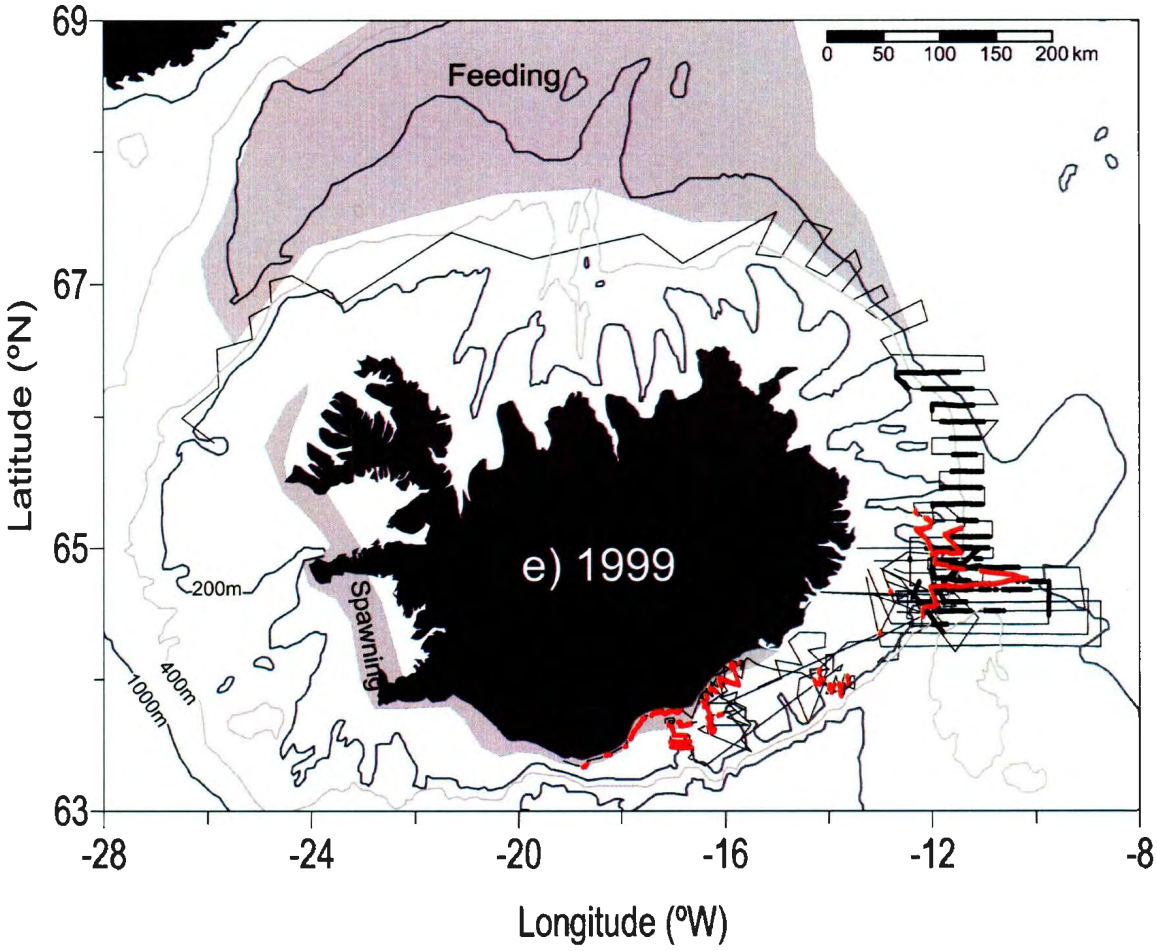

Figure 3.3e. The study region, survey tracks (narrow black line) and location of the spawning migration in January (black dots), February (red dots) and March (green dots) in Icelandic waters from 1992 to 2007. Years 1994, 1996 and 1997 are missing as no surveys were conducted. The western and eastern migration routes bifurcate at 19.25 °W north of Iceland. Spawning grounds (light grey) redrawn from Vilhjálmsson (1994). Summer feeding area (light gray) extends north to 72 °N based on Vilhjálmsson (1994) and Vilhjálmsson and Carscadden (2002). 200 m, 400 m and 1000 m depth contours displayed (gray lines).

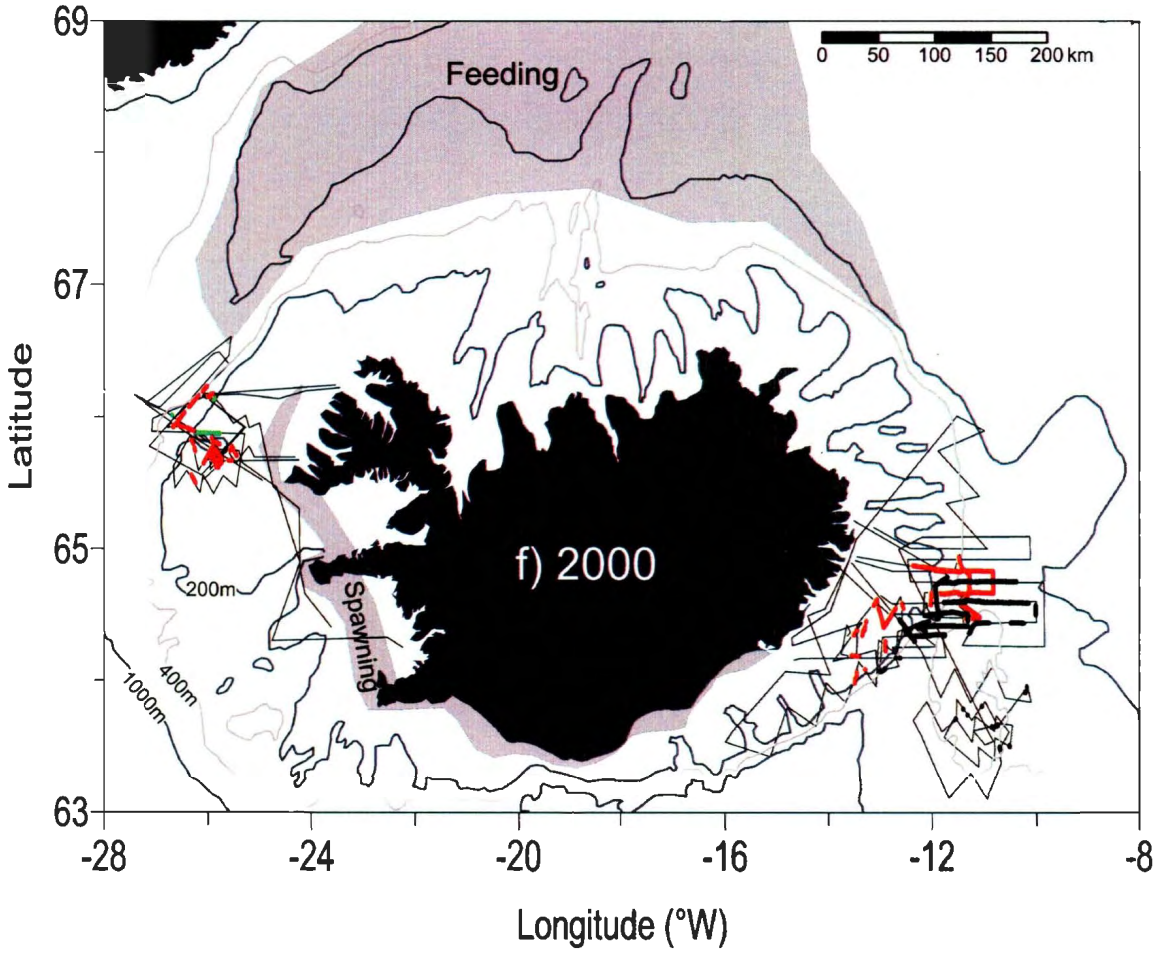

Figure 3.3f. The study region, survey tracks (narrow black line) and location of the spawning migration in January (black dots), February (red dots) and March (green dots) in Icelandic waters from 1992 to 2007. Years 1994, 1996 and 1997 are missing as no surveys were conducted. The western and eastern migration routes bifurcate at 19.25 °W north of Iceland. Spawning grounds (light grey) redrawn from Vilhjálmsson (1994). Summer feeding area (light gray) extends north to 72 °N based on Vilhjálmsson (1994) and Vilhjálmsson and Carscadden (2002). 200 m, 400 m and 1000 m depth contours displayed (gray lines).

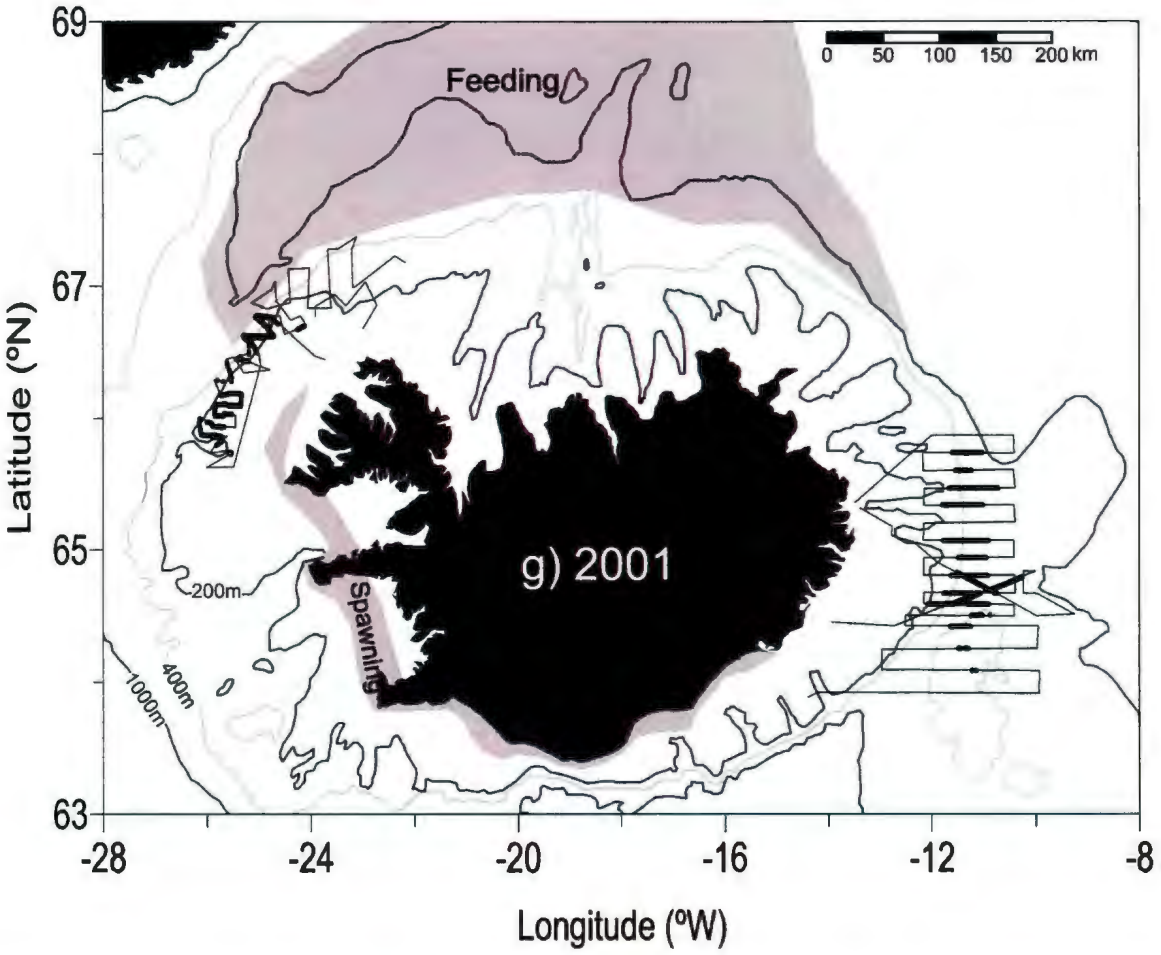

Figure 3.3g. The study region, survey tracks (narrow black line) and location of the spawning migration in January (black dots), February (red dots) and March (green dots) in Icelandic waters from 1992 to 2007. Years 1994, 1996 and 1997 are missing as no surveys were conducted. The western and eastern migration routes bifurcate at 19.25 °W north of Iceland. Spawning grounds (light grey) redrawn from Vilhjálmsson (1994). Summer feeding area (light gray) extends north to 72 °N based on Vilhjálmsson (1994) and Vilhjálmsson and Carscadden (2002). 200 m, 400 m and 1000 m depth contours displayed (gray lines).

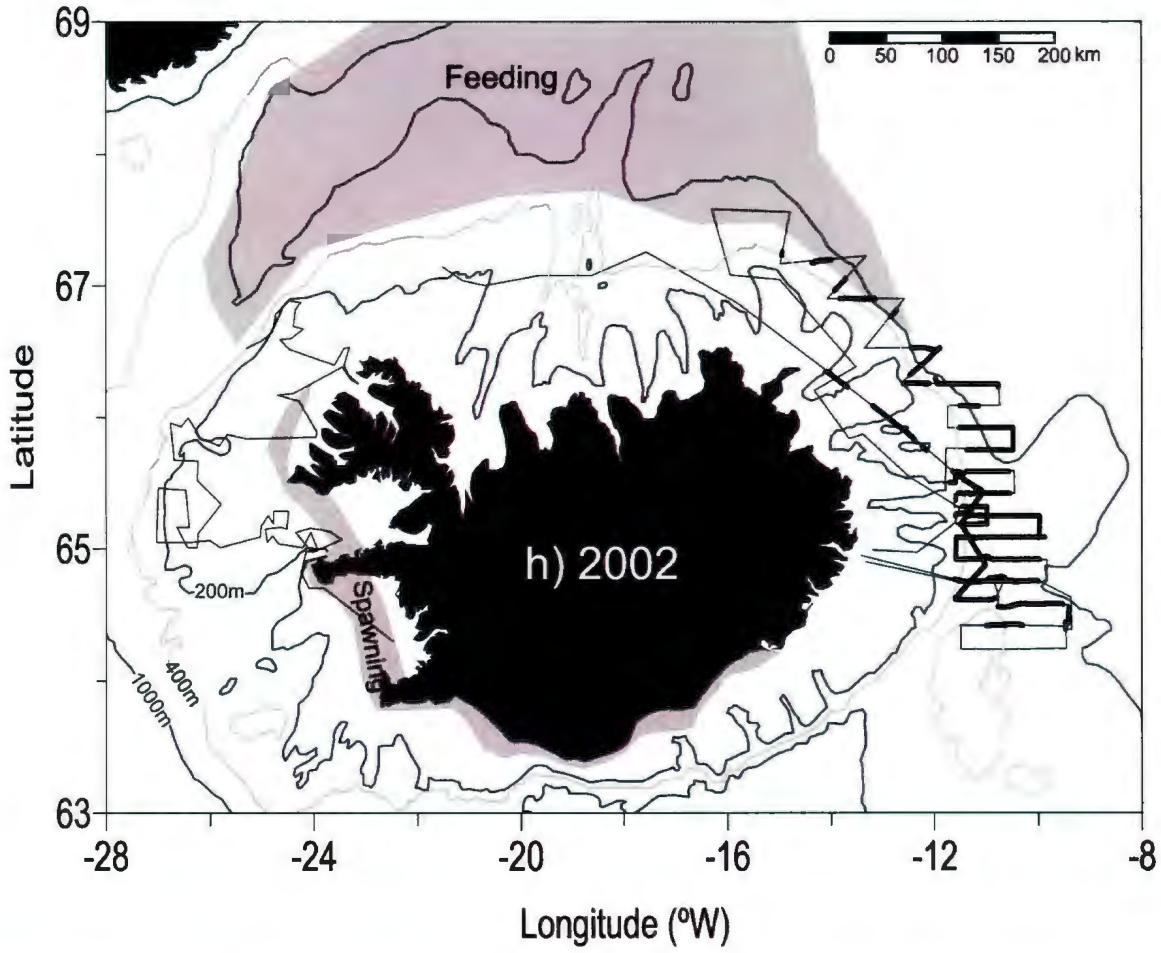

Figure 3.3h. The study region, survey tracks (narrow black line) and location of the spawning migration in January (black dots), February (red dots) and March (green dots) in Icelandic waters from 1992 to 2007. Years 1994, 1996 and 1997 are missing as no surveys were conducted. The western and eastern migration routes bifurcate at 19.25 °W north of Iceland. Spawning grounds (light grey) redrawn from Vilhjálmsson (1994). Summer feeding area (light gray) extends north to 72 °N based on Vilhjálmsson (1994) and Vilhjálmsson and Carscadden (2002). 200 m, 400 m and 1000 m depth contours displayed (gray lines).

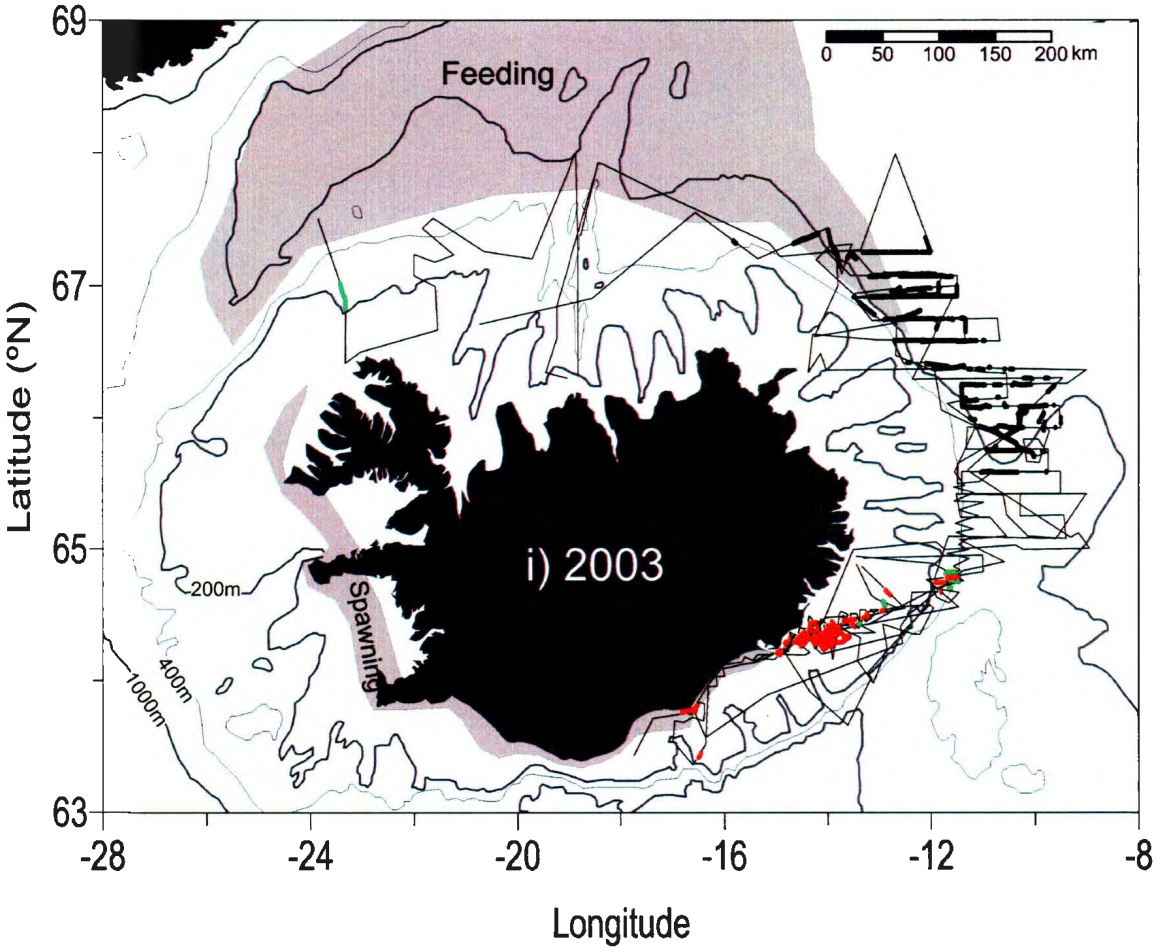

Figure 3.3i. The study region, survey tracks (narrow black line) and location of the spawning migration in January (black dots), February (red dots) and March (green dots) in Icelandic waters from 1992 to 2007. Years 1994, 1996 and 1997 are missing as no surveys were conducted. The western and eastern migration routes bifurcate at 19.25 °W north of Iceland. Spawning grounds (light grey) redrawn from Vilhjálmsson (1994). Summer feeding area (light gray) extends north to 72 °N based on Vilhjálmsson (1994) and Vilhjálmsson and Carscadden (2002). 200 m, 400 m and 1000 m depth contours displayed (gray lines).

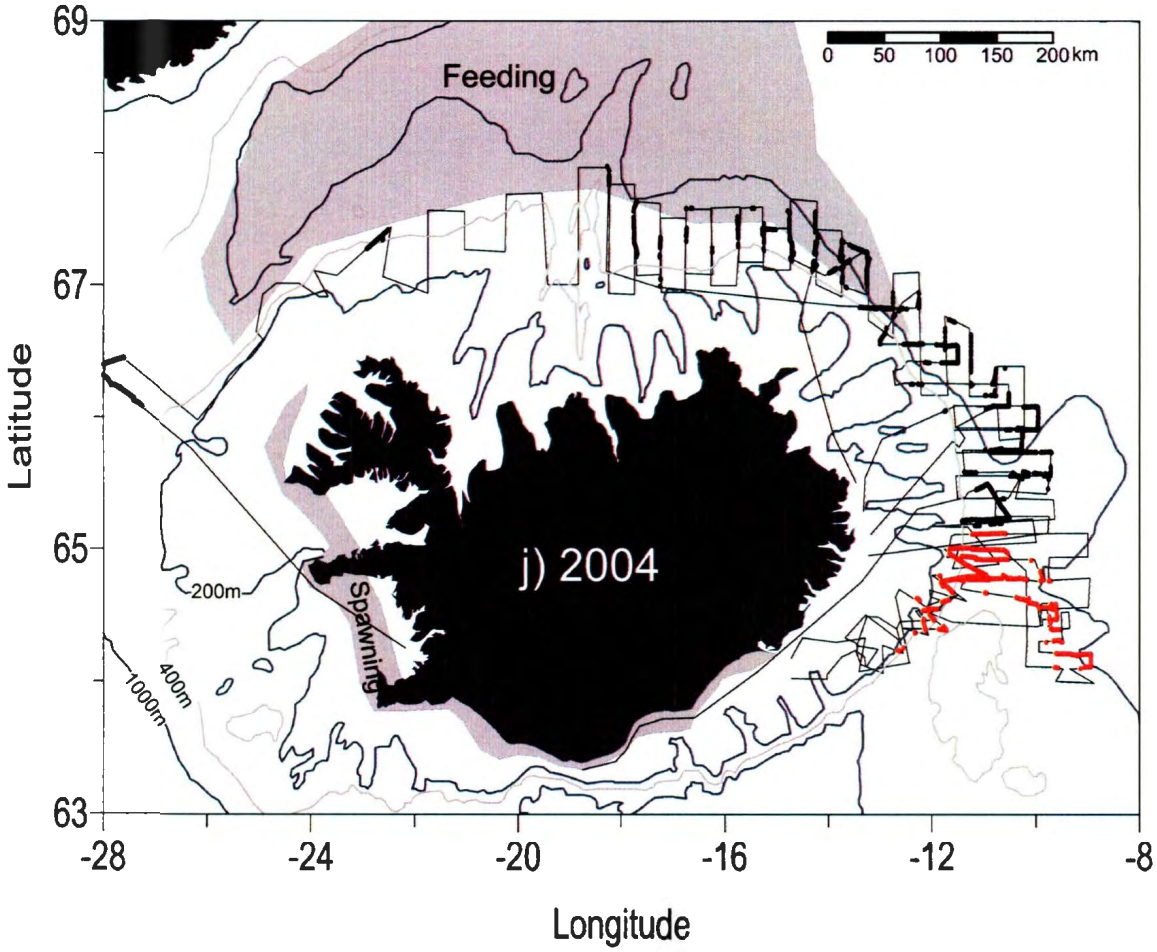

Figure 3.3j. The study region, survey tracks (narrow black line) and location of the spawning migration in January (black dots), February (red dots) and March (green dots) in Icelandic waters from 1992 to 2007. Years 1994, 1996 and 1997 are missing as no surveys were conducted. The western and eastern migration routes bifurcate at 19.25 °W north of Iceland. Spawning grounds (light grey) redrawn from Vilhjálmsson (1994). Summer feeding area (light gray) extends north to 72 °N based on Vilhjálmsson (1994) and Vilhjálmsson and Carscadden (2002). 200 m, 400 m and 1000 m depth contours displayed (gray lines).

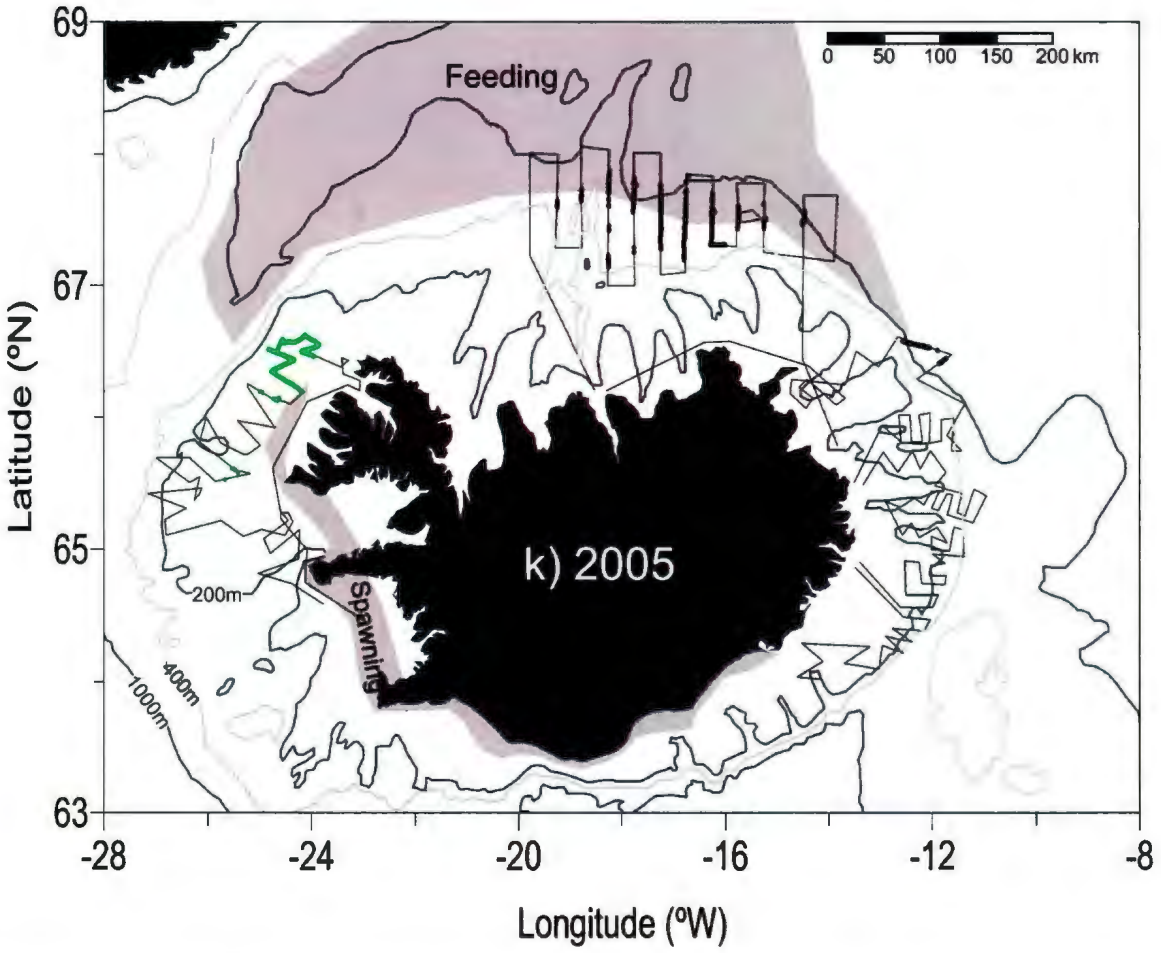

Figure 3.3k. The study region, survey tracks (narrow black line) and location of the spawning migration in January (black dots), February (red dots) and March (green dots) in Icelandic waters from 1992 to 2007. Years 1994, 1996 and 1997 are missing as no surveys were conducted. The western and eastern migration routes bifurcate at 19.25 °W north of Iceland. Spawning grounds (light grey) redrawn from Vilhjálmsson (1994). Summer feeding area (light gray) extends north to 72 °N based on Vilhjálmsson (1994) displayed (gray lines).

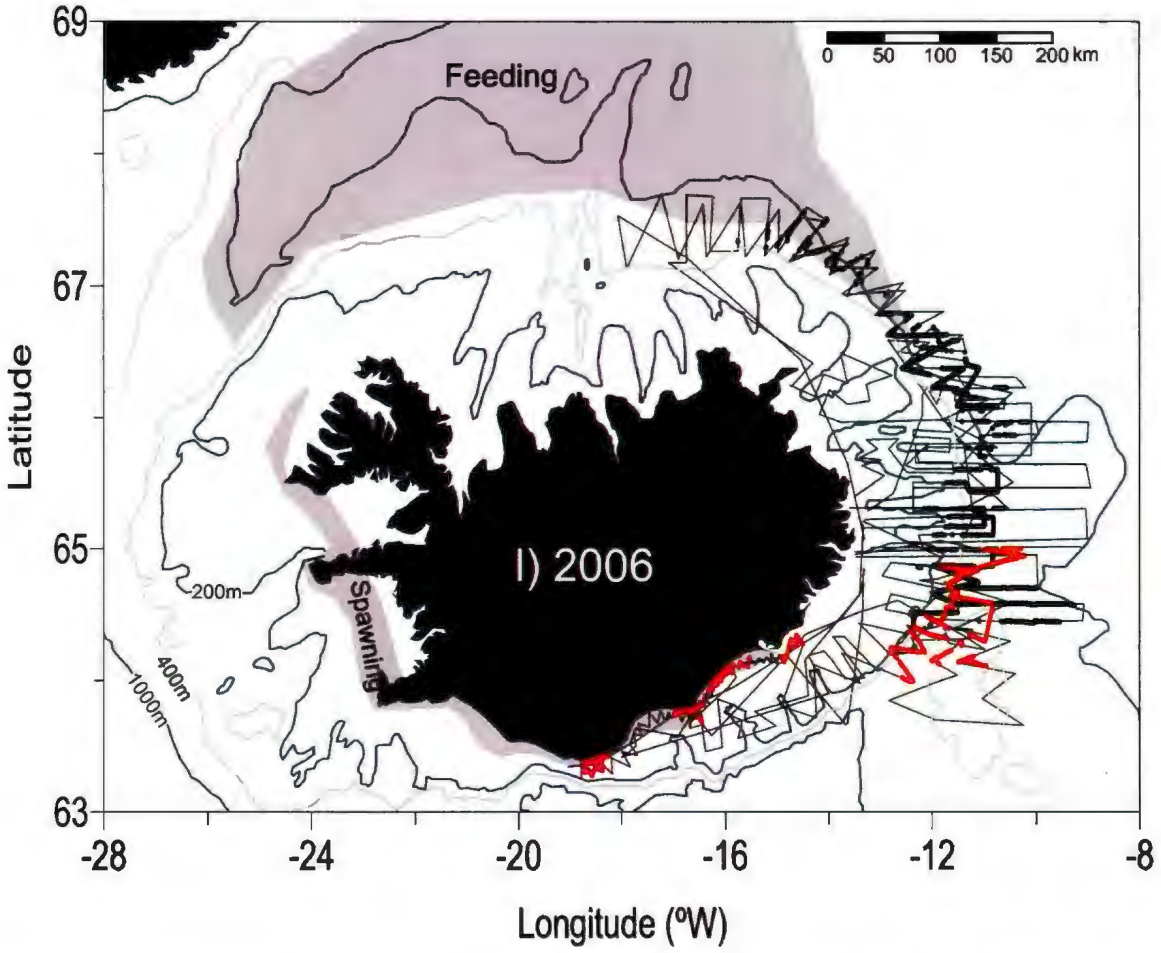

Figure 3.3l. The study region, survey tracks (narrow black line) and location of the spawning migration in January (black dots), February (red dots) and March (green dots) in Icelandic waters from 1992 to 2007. Years 1994, 1996 and 1997 are missing as no surveys were conducted. The western and eastern migration routes bifurcate at 19.25 °W north of Iceland. Spawning grounds (light grey) redrawn from Vilhjálmsson (1994). Summer feeding area (light gray) extends north to 72 °N based on Vilhjálmsson (1994) and Vilhjálmsson and Carscadden (2002). 200 m, 400 m and 1000 m depth contours displayed (gray lines).

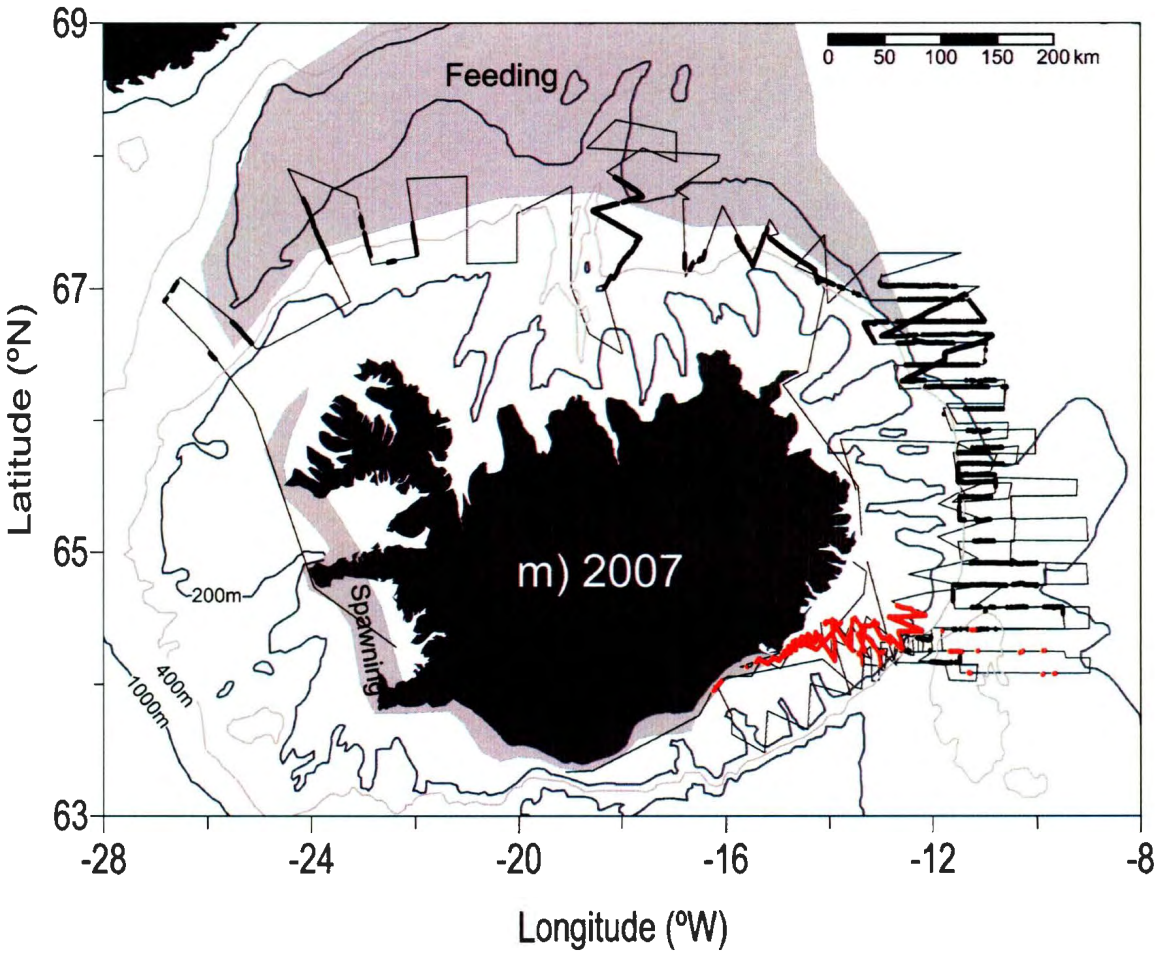

Figure 3.3m. The study region, survey tracks (narrow black line) and location of the spawning migration in January (black dots), February (red dots) and March (green dots) in Icelandic waters from 1992 to 2007. Years 1994, 1996 and 1997 are missing as no surveys were conducted. The western and eastern migration routes bifurcate at 19.25 °W north of Iceland. Spawning grounds (light grey) redrawn from Vilhjálmsson (1994). Summer feeding area (light gray) extends north to 72 °N based on Vilhjálmsson (1994) and Vilhjálmsson and Carscadden (2002). 200 m, 400 m and 1000 m depth contours displayed (gray lines).

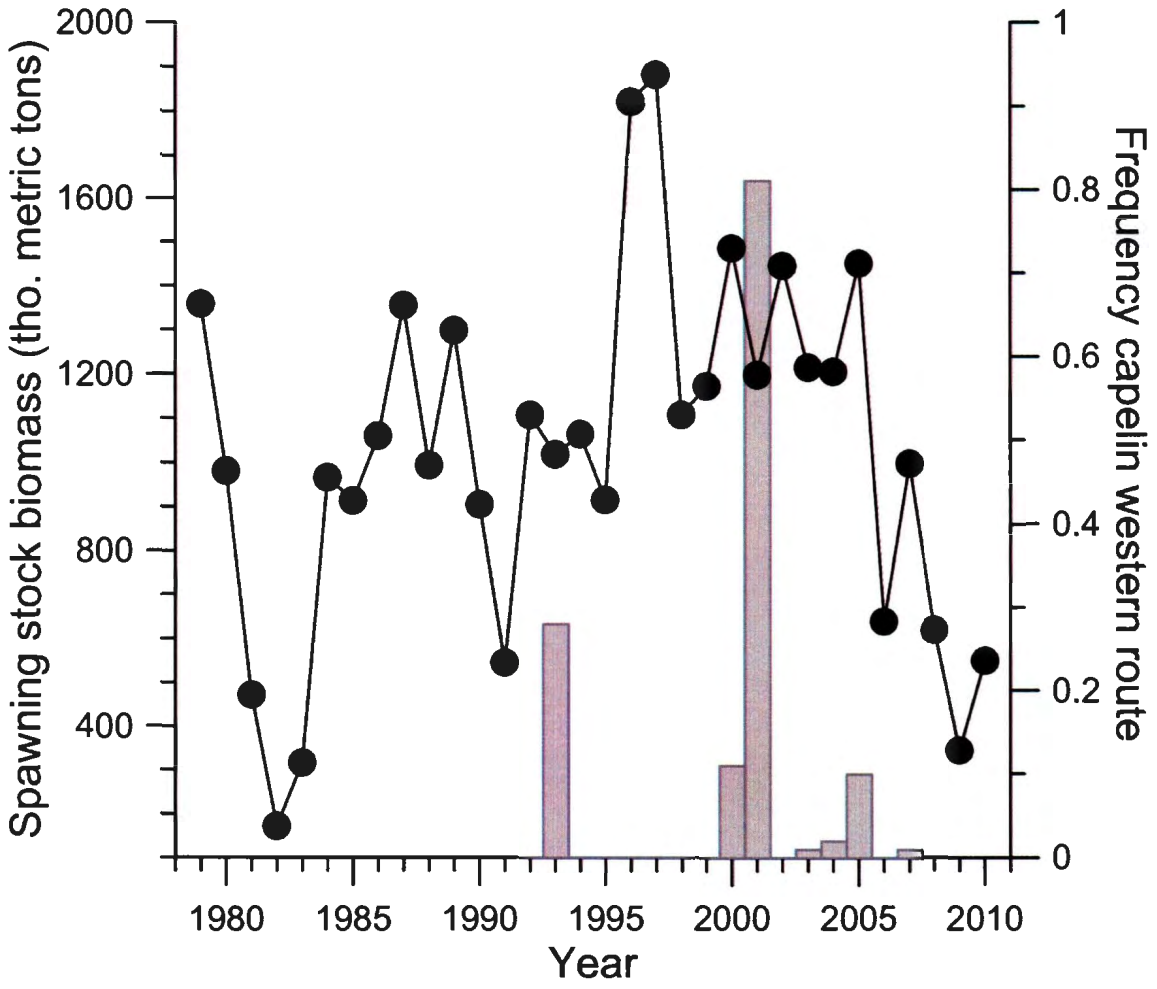

Figure 3.4. Estimated capelin spawning stock biomass on January 1st (filled circle) calculated from fall or winter capelin acoustic surveys (Anon., 2010; Table 3.21.5) and relative proportions (filled bar), acoustic estimates from Appendix I, of the annual spawning cohort which used the western spawning migration route. The average SSB, from 1979 to 2010, is 1017 thousand metric tons.

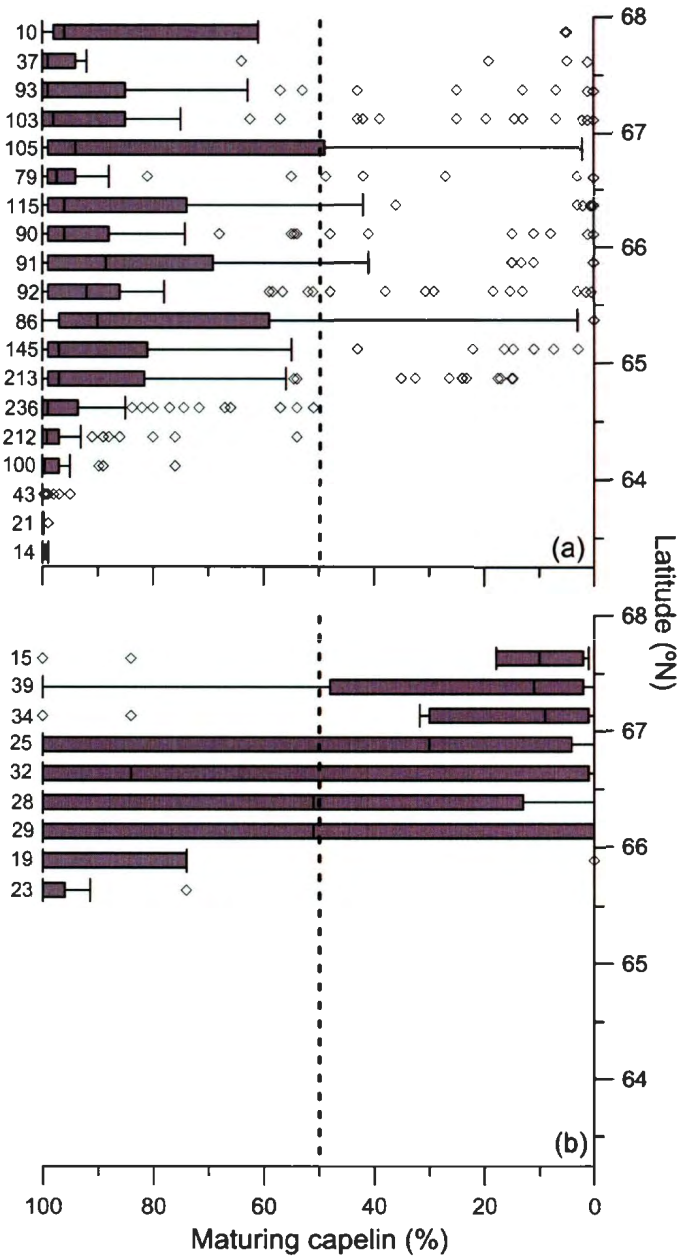

Figure 3.5. Box plot of percentage of maturing capelin binned into 0.25 ° latitude/longitude bins along the eastern (a; n = 1885 bins) and western migration routes (b; n = 244 bins) for all years, 1992 – 2007 (excluding 1994, 1996 and 1997). First and third quartiles, median (horizontal line within box), maximum and minimum (whiskers) and outliers (> 1.5 interquartile ranges (open diamonds)) shown. N longitude bins per latitude bin displayed left of whisker.

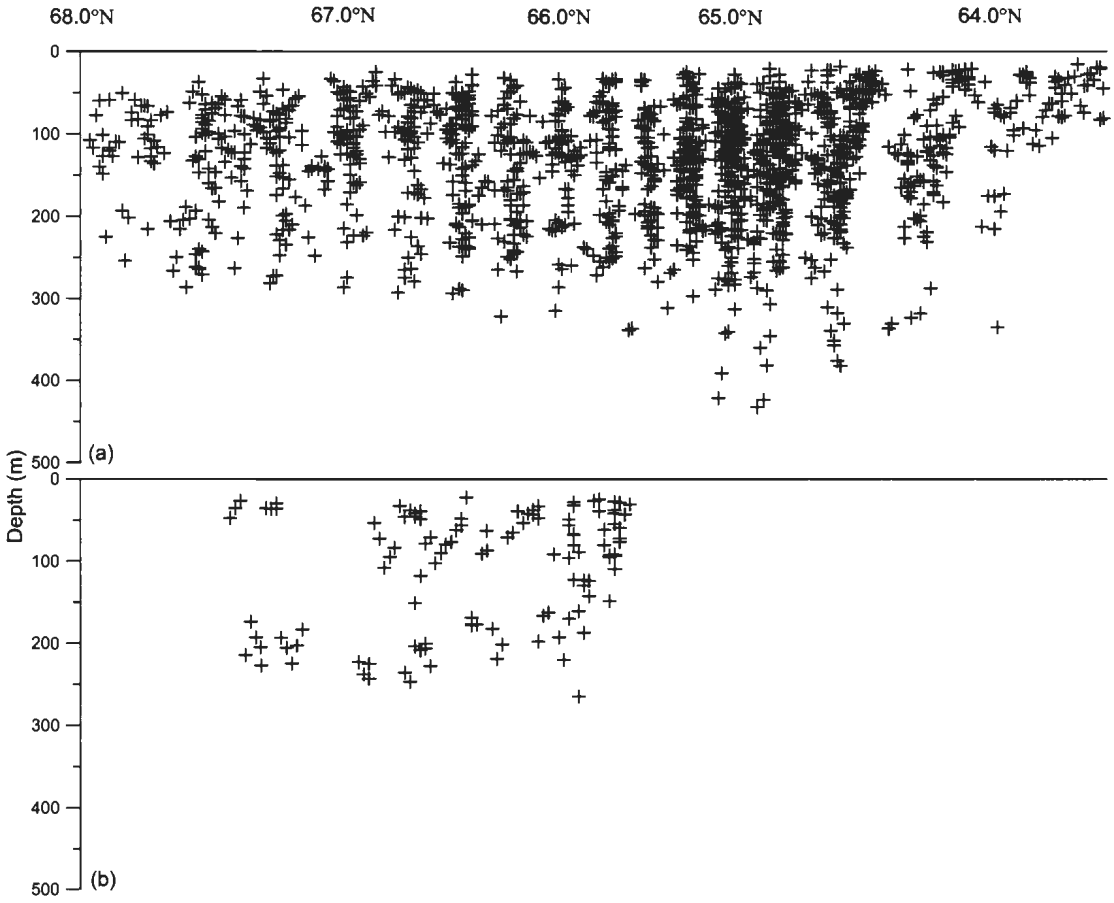

Figure 3.6. Weighted average depth of capelin, by acoustic density, for each 0.25 ° latitude/longitude bin, for the east (a; n = 1681 bins) and the west migrations (b; n = 118 bins) for all years, 1992 – 2007 (excluding 1994, 1996 and 1997).

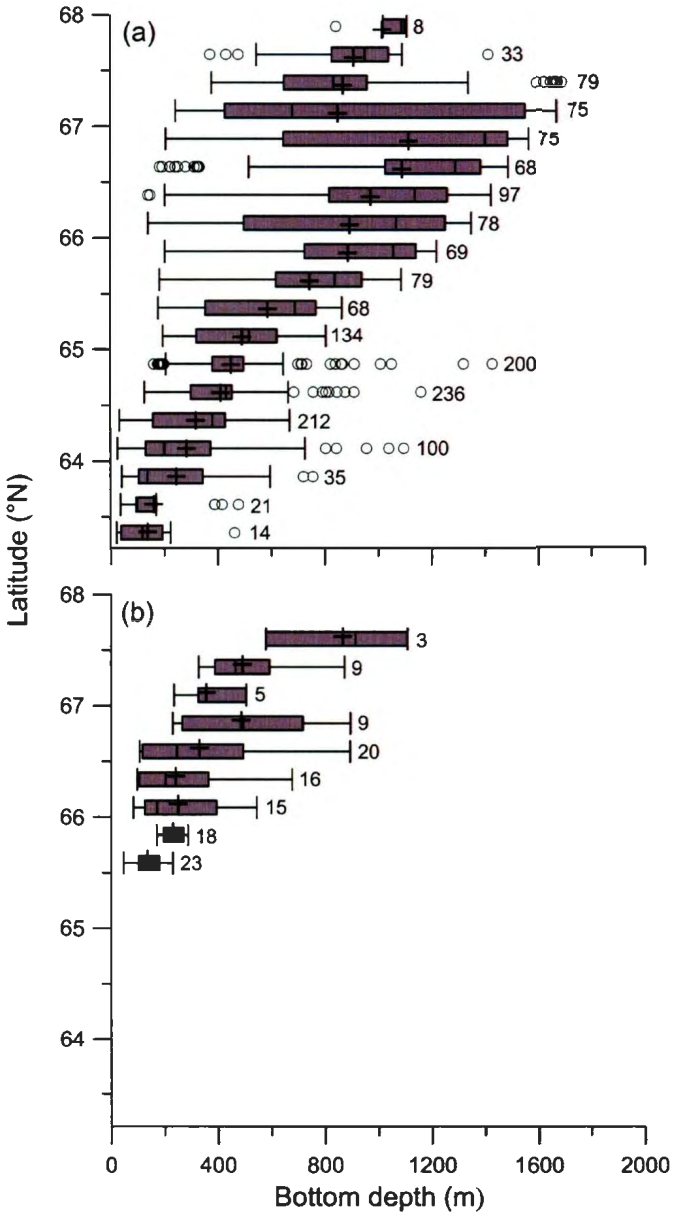

Figure 3.7. Box plot of bottom depth where capelin were located along the eastern (a; n = 1681 bins) and western migration routes (b; n = 118 bins) for all years, 1992 – 2007 (excluding 1994, 1996 and 1997). First and third quartiles, median (horizontal line within box), maximum and minimum (whiskers), average (cross) and outliers (> 1.5 interquartile range (open diamonds)) shown. N longitude bins per latitude bin displayed next of whisker.

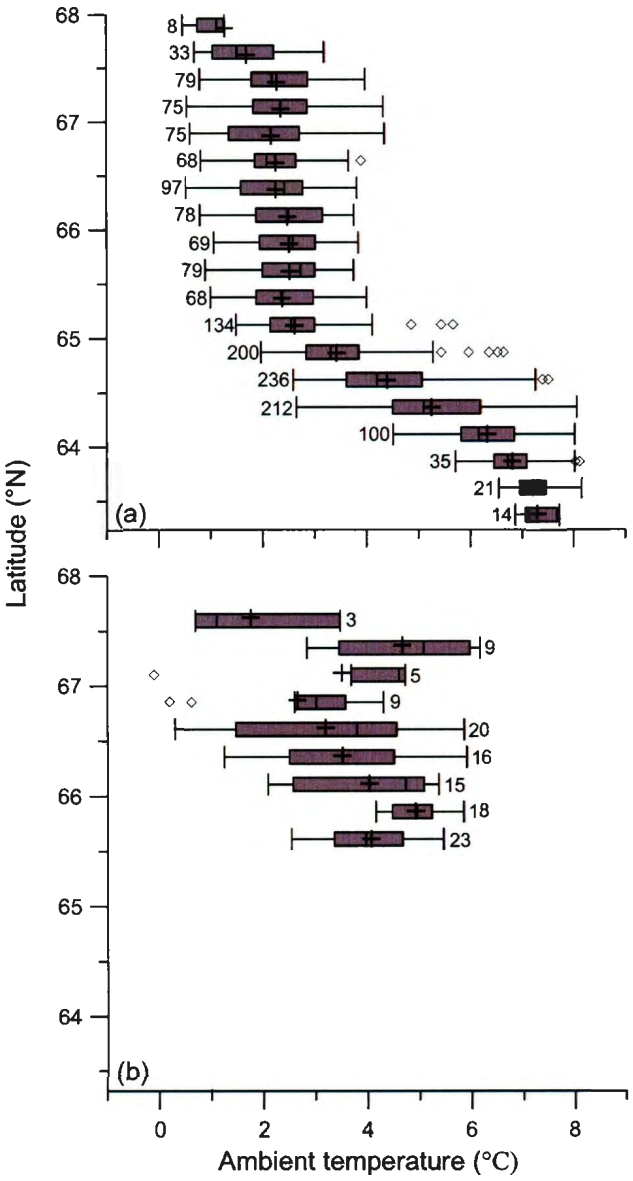

Figure 3.8. Box plot of ambient temperature where capelin were located along the eastern (a; n = 1681 bins) and western migration routes (b; n = 118 bins) for all years, 1992 – 2007 (excluding 1994, 1996 and 1997). First and third quartiles, median (horizontal line within box), maximum and minimum (whiskers), average (cross) and outliers (> 1.5 interquartile range (open diamonds)) shown. N longitude bins per latitude bin displayed next of whisker.

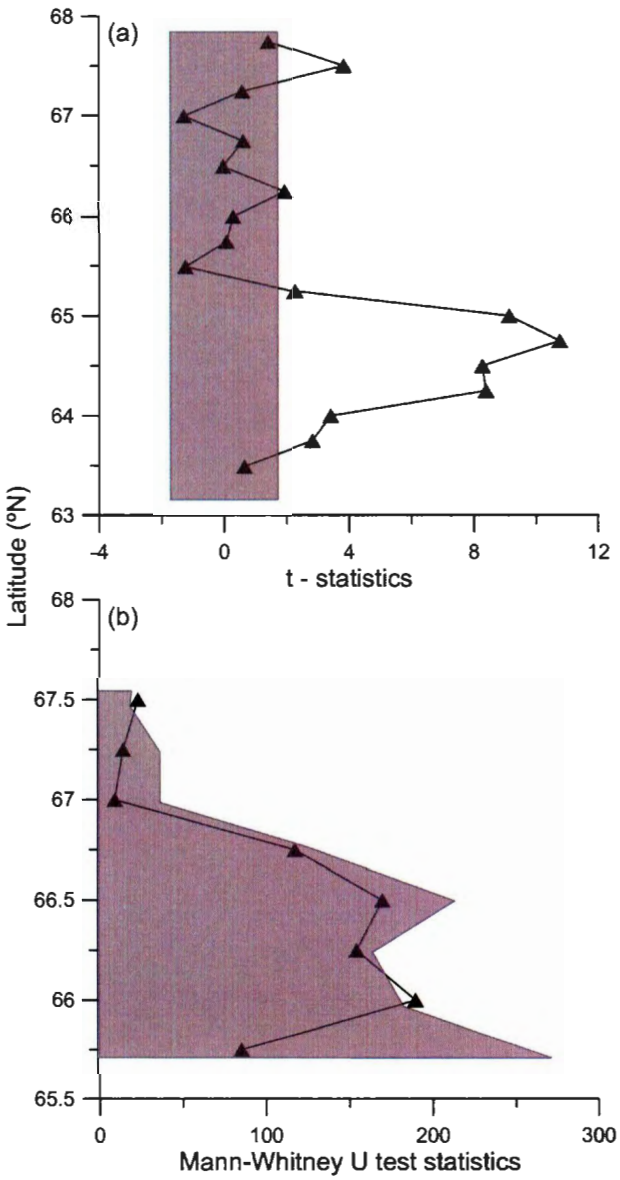

Figure 3.9. Comparison of temperatures between adjacent 0.25 ° latitude bins along the north-to-south migration axis for all years, 1992 – 2007 (excluding 1994, 1996 and 1997). One-tailed T-Test assuming greater temperature at a more southern location used for the eastern migration route (a) but one-tailed non-parametric Mann-Whitney test for the western route (b) due to unequal variance between latitudes. Shaded areas present location of no difference ($p > 0.05$) in temperature between adjacent latitude bins.

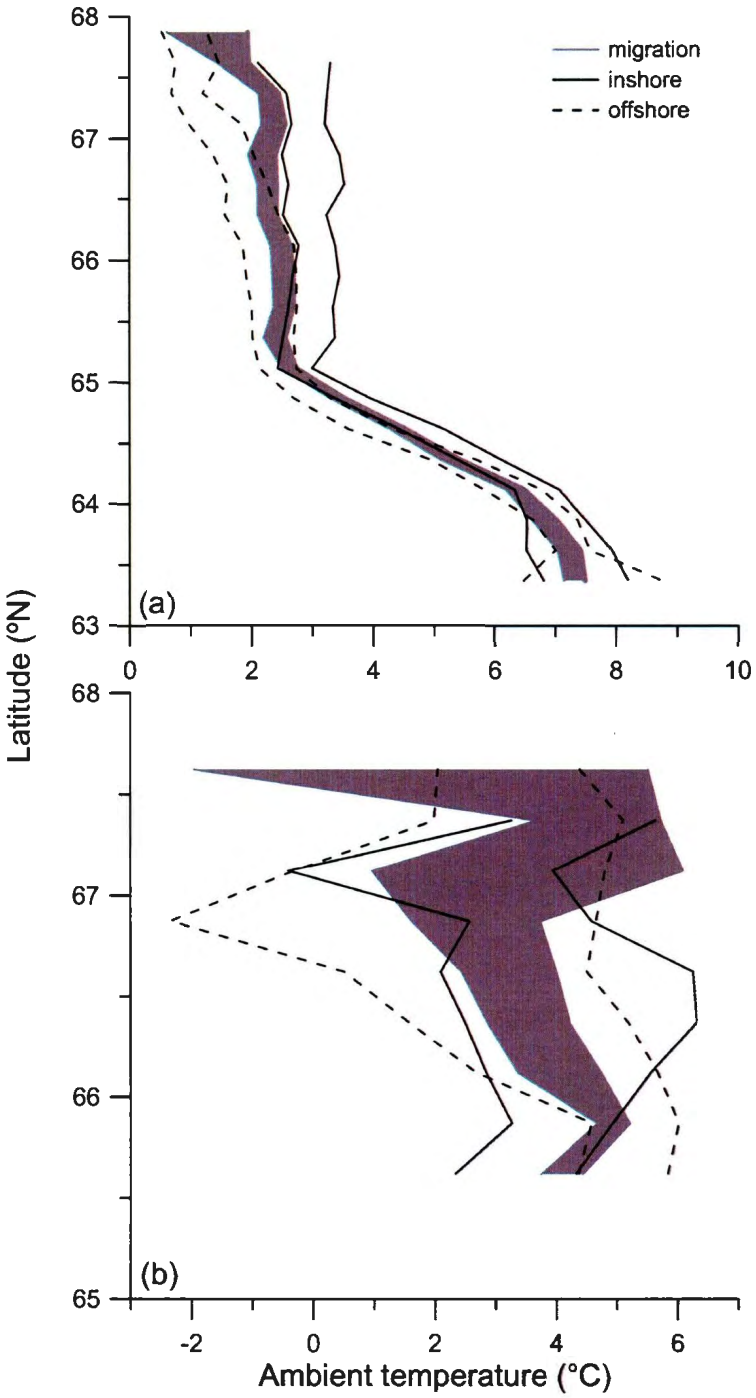

Figure 3.10. Ninety-five-percent confidence intervals for the average ambient temperature where capelin were located (shaded area) and inshore (solid line) and offshore (broken line) from the migration for the eastern (a) and the western routes (b) for all years, 1992 – 2007 (excluding 1994, 1996 and 1997).

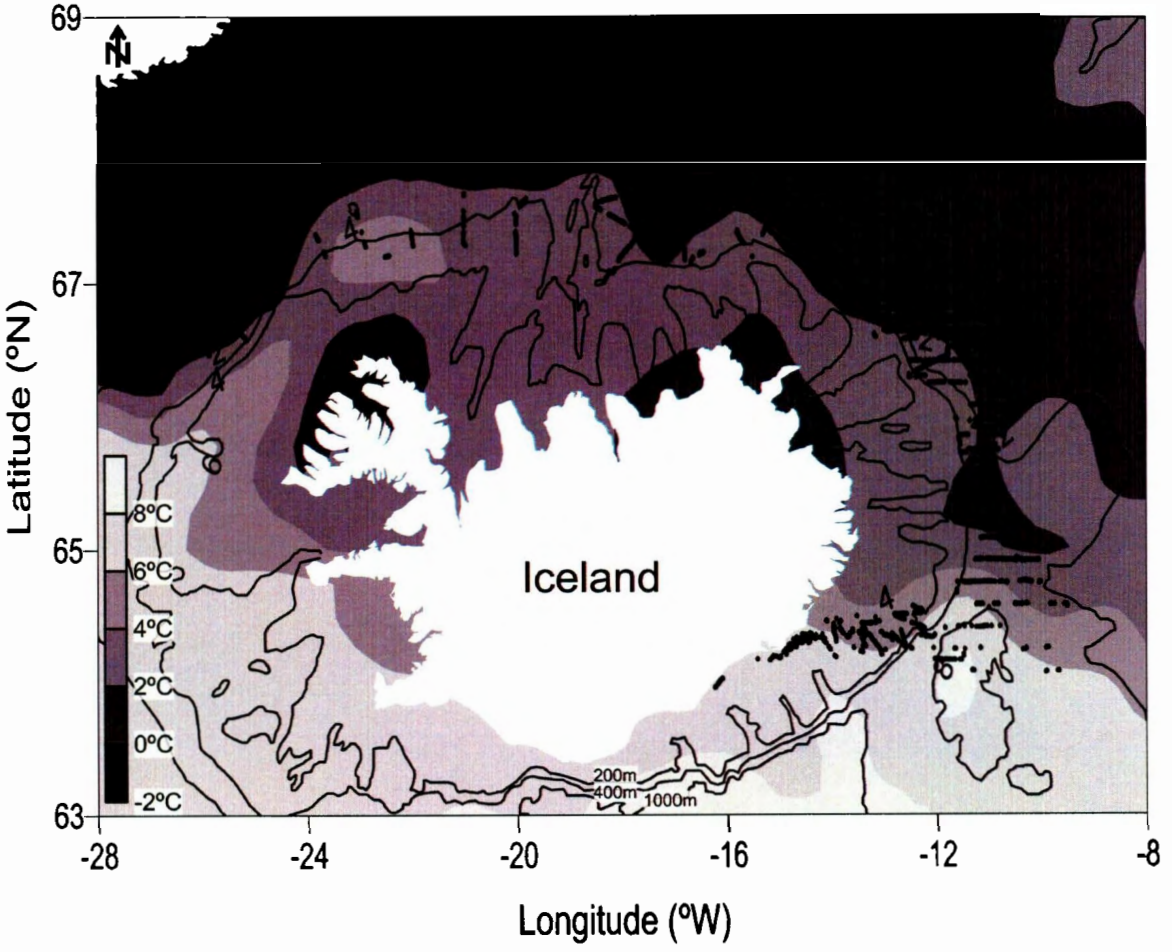

Figure 3.11. Sea surface temperature (°C) on January 22, 2007, and location of the capelin spawning migration in 2007, 3 January – 15 February (black dots). Depth contours 200 m, 400 m and 1000 m displayed (grey lines).

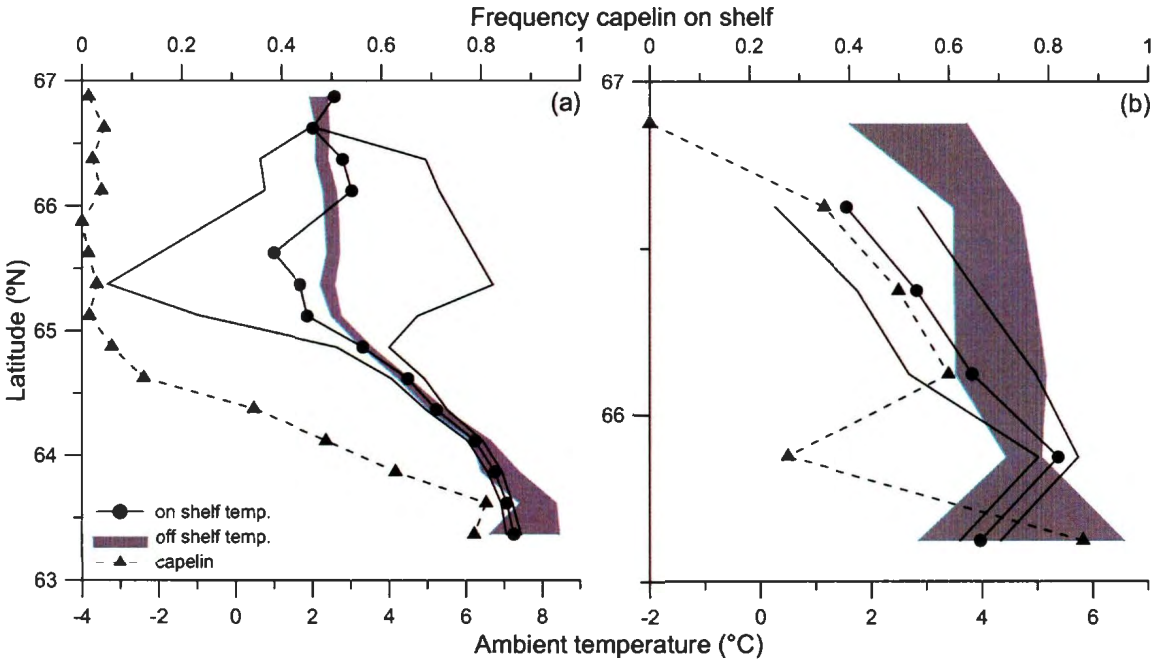

Figure 3.12. Ninety-five-percent confidence intervals (CI) for the average ambient temperature where capelin were located: off the shelf (shaded area) and on the shelf (< 200 m bottom depth; filled circle (mean); solid lines (95 % CI)); and frequency of capelin located on the shelf (filled triangle) for eastern (a) and western (b) migration routes for all years, 1992 – 2007 (excluding 1994, 1996 and 1997). No shelf area exists north of 67°N.

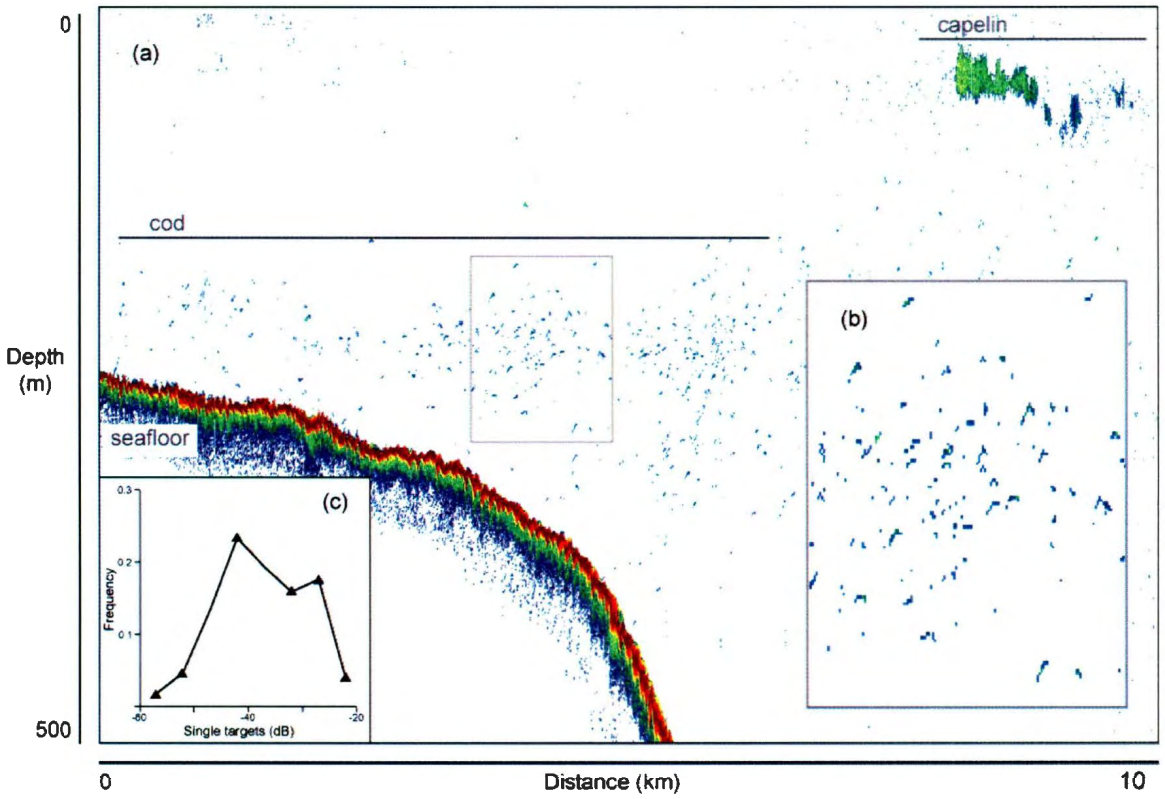

Figure 3.13. Echogram (a; 38 kHz S_v) with capelin located off the shelf and cod on the shelf (single targets: -60 to -20 dB; Rose and Porter, 1996). Echogram is from 23. January 2006, 1 am, location 66.78 ° N and 13.05 ° W. Cod single targets enlarged (b) from rectangular box in (a) and frequency of single targets (c; n = 403) within the enlarged area.

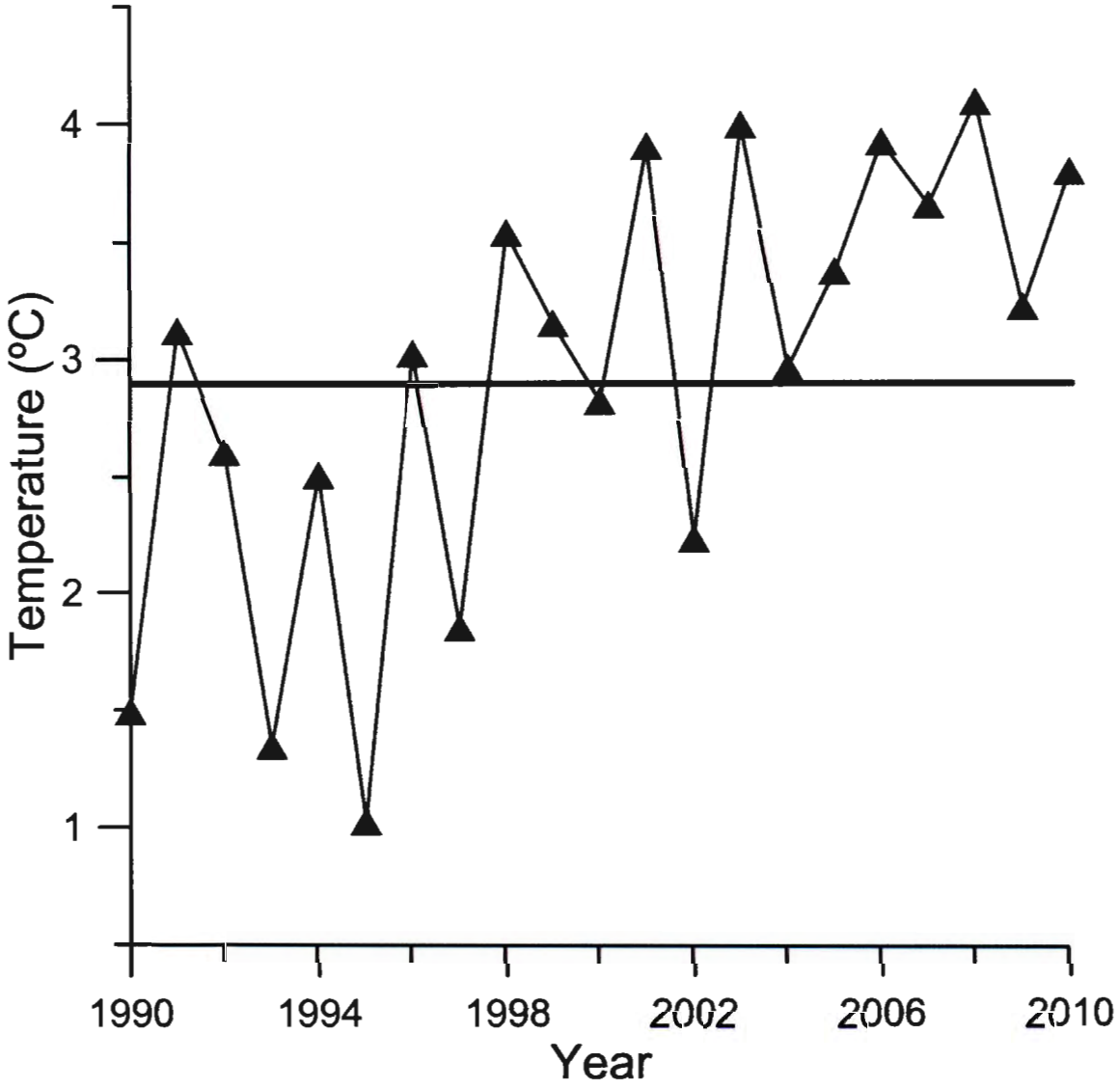

Figure 3.14. Average temperature in the surface 200 meters on the shelf north of Iceland, Siglunes hydrographical section (bold vertical line; in Fig. 3.1), in February. Years 2008 – 2010 were included to show continuing warming trend of winter temperatures. Capelin spawned on the south coast in 2008 – 2010 (Anon, 2008, 2009, 2010). Average temperature for the 21-year period was 2.9 °C (horizontal line).

3.10 Appendix

Appendix 3.1. Capelin winter acoustic assessment surveys. No surveys conducted in 1994, 1996 and 1997. Research vessels: Bjarni Saemundsson (BS) 35 m long , Arni Fridriksson RE100 (AF RE100) 25 m, commission stopped in 2000, and Arni Fridriksson RE200 (AF RE200) 70 m long. Abundance was calculated as number of capelin located in the acoustic beam and not extrapolated to present a larger area. Capelin were recorded on the major eastern (E) and the minor western (W) spawning migration route.

Year	Date	Survey track (km)	Biological samples (n)	Acoustic abundance (fish / m^2)	Migration route	Research vessel
1992	4 -16 Jan.	3764	22	19,029	E	AF RE100
1993	5 – 20 Jan.	4877	13	6404	E	BS
	5 – 11 Mar.	2691	8	2459	W	AF RE100
1995	4 – 15 Jan.	2202	17	8336	E	AF RE100
	20 – 25 Jan	1374	10	1356	E	AF RE100
	3 – 27 Jan.	3980	24	5325	E	BS
	2 – 16 Feb.	2992	24	14,844	E	AF RE100
	9 – 16 Feb.	2324	31	17,285	E	BS
1998	22 – 27 Jan.	1749	7	1631	E	BS
1999	14 – 27 Jan.	3578	22	15,855	E	BS
	14 – 15 Jan.	303	2	5767	E	AF RE100
	21 – 29 Jan.	1331	18	5773	E	AF RE100

	6 – 17 Feb.	1994	36	54,144	E	AF RE100
2000	18 Jan.-9 Feb.	4913	43	27,615	E	BS
	16 – 19 Feb.	947	2	338	W	BS
	24 Feb-2 Mar.	725	2	3375	E	AF RE100
2001	14 -24 Jan.	2414	13	5033	E	BS
	24 -31 Jan.	1070	14	21,400	W	AF RE200
2002	9 – 20 Jan.	3272	23	37,148	E	AF RE200
	13 – 20 Mar.	1902	2*	0	W	AF RE200
2003	6 – 23 Jan.	4850	23	29,554	E	AF RE200
	17 Feb. – 10 Mar.	3380	25	44,656	E and W	AF RE200
2004	3 – 12 Jan.	3095	18	3550	E and W	AF RE200
	19 – 30 Jan.	4031	12	26,810	E	AF RE200
	10 – 17 Feb.	2272	21	44,270	E	AF RE200
2005	4 – 18 Jan.	1984	4	27,985	E	AF RE200
	5 – 10 Mar.	1303	8	3264	W	AF RE200
2006	3 Jan – 2 Feb.	6577	23	19,722	E	AF RE200
	6 – 17 Feb.	2619	6	2,481,896	E	AF RE200
	8 – 15 Feb.	83	1	24,354	E	BS
2007	3 - 12 Jan.	1966	10	12,173	E and W	AF RE200
	23 – 31 Jan.	3181	12	43,948	E	AF RE200
	6 – 15 Feb.	3172	4	44,581	E	AF RE200

* Fishing by commercial vessel in the same area.

Chapter 4. Staged spawning migration in Icelandic capelin (*Mallotus villosus*): effects of temperature, stock size and maturity.

4.1 Abstract

Capelin (*Mallotus villosus*) is the largest commercial fish stock in Icelandic waters and also an important forage fish. Every winter pre-spawning capelin migrate 500 to 1000 km from their offshore (>200m bottom depth) northern feeding areas (67–71°N) to inshore (<200m bottom depth) southern spawning areas (63–65°N). The major migration route is east of Iceland, consisting of both offshore and inshore phases. The migration begins (50% of spawning stock biomass passed latitude 67°N) offshore as capelin skirt the shelf edge north of 65°N then veer inshore between latitudes 64–65°N. Hydro-acoustic data from 1992 to 2007 (excluding 1994, 1996, 1997 and 2005) demonstrated that, for the offshore phase, migration timing varied by as much as one month, from December 22 to January 21. A combination of larger spawning stock biomass and colder feeding ground temperatures (August to December) corresponded to earlier offshore migration. The timing of the inshore migration phase was not dependent on the offshore migration timing, and never began prior to the first week of February. Many cohorts arrived at latitudes 64–65°N in early January but staged offshore at latitudes 63.8–65.8°N until early February. The longest observed delay in the staging area was five weeks before the inshore phase was initiated. Timing of the inshore migration was controlled by gonad maturity, with migration beginning when roe content attained 12–14%. Staging limited the time capelin spent on the continental shelf before spawning to three weeks. I suggest that offshore staging evolved to minimize temporal overlap with predatory cod.

Key words: capelin, *Mallotus villosus*, spawning migration, cue mechanism, staging, gonad maturity, temperature, spawning stock biomass.

4.2 Introduction

Capelin (*Mallotus villosus*) are a small (12 – 20 cm at maturity) schooling pelagic fish with circumpolar distribution (Vilhjálmsson, 1994). In Icelandic waters, capelin undertake an annual spawning migration each winter that covers 500 – 1000 km from northern summer feeding areas in the Iceland Sea (67 – 71 °N; Vilhjálmsson, 2002) to coastal spawning waters (<200 m bottom depth) south and west of Iceland (Vilhjálmsson, 1994; Olafsdottir and Rose, 2012). This migration has been monitored annually since the late 1970s as a result of its commercial and biological importance (Vilhjálmsson, 2002). Of note, capelin utilize a well defined southward migration route in most years, which skirts the eastern edge of the continental shelf until warm (> 4.5 °C) Atlantic Ocean waters are encountered between latitudes 64 – 65 °N (Olafsdottir and Rose, 2012). Thereafter, capelin migrate inshore to spawn. Early phases of the migration appear to vary temporally, with the leading edge of the migration reported to reach latitude 64 °N at variable times during January (Vilhjálmsson, 1994; Olafsdottir and Rose, 2012). Such temporal variability in the early phases of migration does not appear to influence the timing of the final phase of the migration onto the continental shelf as capelin have never been located in inshore waters before February. These reports suggest that migration by capelin is not constant and continuous, and that a staging area may exist that is used prior to the final migration to the spawning grounds.

Long-distance migrations of birds utilize staging areas at specific locations along the migration route (Elphick, 1995). Staging areas are vital for birds to replenish their

energy reserves before beginning the next phase of their migration and for successful breeding (Ebbinge and Spaans, 1995). Although many fish species also conduct extended seasonal migrations, staging areas for fish migration are not extensively documented. Staging has been recorded in several anadromous fish species having long-distance spawning migrations (Hodgson and Quinn, 2002; High *et al.*, 2006; Mundy and Evenson, 2011). In those species, the location of staging areas is variable, ranging from oceanic sites close to the spawning river (Mundy and Evenson, 2011) to in-river staging areas close to the spawning site (Hodgson and Quinn, 2002; High *et al.*, 2006). In-river staging has been linked to water temperatures (Hodgson and Quinn, 2002; High *et al.*, 2006). Davoren *et al.* (2006) suggested that a staged migration of maturing capelin was occurring in a coastal region of Newfoundland with the same staging location used in consecutive years. The role of staging in fish migrations is poorly understood.

The evolution of staging behaviour on spawning migration routes infers that there is a fitness advantage to staging for the pre-spawning fish. In capelin, gonad maturation progresses through the winter months and spawning occurs when roe content reaches 25 – 30 %, typically from late February to early April (Vilhjálmsson, 1994). Offshore staging could have evolved to enable gonad maturity to reach a specific threshold before capelin cross the continental shelf, as they do each year after they encounter warm Atlantic waters (> 4.5 °C) between latitudes 64 - 65 °N (Olafsdottir and Rose, 2012). But why they would remain offshore when they could just as easily move inshore and await maturation. One possibility is that the shelf and inshore waters have much higher abundances of predatory fish, particularly Atlantic cod (*Gadus morhua*), than do potential offshore staging areas (Begg and Marteinsdottir, 2002; Anon, 2010). Under this

hypothesis, the time spent in coastal waters would be minimized, as would exposure to predation, hence, could increase survival and fitness of capelin. Of note, cod is the dominant predator of capelin in Icelandic waters (Vilhjálmsson, 2002) and capelin are the single most important prey for cod (Pálsson 1997; Pálsson and Björnsson, 2011). During the inshore phase of the capelin spawning migration, when capelin and cod distributions overlap, capelin constitute on average 70 % by weight of total consumption of cod (Pálsson 1997). By minimizing their time inshore capelin may increase survival by reducing cod predation until spawning.

The first objective of this paper is to examine initial cues that influence the timing of Icelandic capelin migrations. Various factors are known to affect migration timing of fish: among them temperature (Carscadden *et al.*, 1997; Hodgeson and Quinn, 2002; High *et al.*, 2006), maturity stage (Shackell *et al.*, 1994) and fish length (Carscadden *et al.*, 1997). I begin by testing a base hypothesis that the winter solstice is a cue for maturing capelin to begin migration. I also assess hypotheses that capelin migrate earlier: 1) in warmer years, 2) when fish size is greater and gonads mature earlier and 3) when stock sizes are larger (density dependent).

The second objective of this paper is to examine the putative presence and location of a staging area on the migration route and factors that may influence the timing of the last phase of the migration and shed light on the function of staging. Finally, I test two hypotheses regarding the final cross-shelf migration phase that takes capelin to their spawning grounds (Olafsdottir and Rose, 2012), namely that encountering warmer temperatures or surpassing a maturity threshold spurs the final migration phase.

4.3 Materials and methods

4.3.1 Acoustic data

The present study uses digitized acoustic data on abundance and distribution of migratory maturing capelin from the winter (January to March) acoustic assessment surveys of the Marine Research Institute, Reykjavik, Iceland. Capelin acoustic surveys have been conducted annually since the late 1970s. In the current paper, all available digital acoustic data collected by three vessels over the 16 year period from 1992 to 2007 are used. Surveys were not conducted in 1994, 1996, 1997 and the 2005 data are not used as surveys were only conducted north of 67 °N. The survey region (Fig. 4.1) was the northwest, north and northeast of Iceland (63 – 68 °N and 8 – 28 °W). Only data from the dominant eastern spawning migration route as defined by Olafsdottir and Rose (2012), south of 67 °N, were used as consequences due to the sporadic use of the western route (see Appendix A in Olafsdottir and Rose, 2012).

All 12 years of data used had one or more acoustic surveys (see Fig. 3 in Olafsdottir and Rose, 2012). In years with multiple surveys the first survey to locate more than 50% of the estimated spawning stock biomass (Anon, 2010) was used to calculate the average encounter date and latitude epicentre (centroid).

Over the 12 years of this study surveying rarely started on the same date, ranging from January 3rd to the 22nd (Table 4.1), making direct comparisons of initial timing of the migration difficult. To overcome this problem, latitude 67 °N was used as a gatepost for assessing the timing of the initial phase of the migration. As an index of migration timing, the date when half the capelin migration passed the 67 °N gatepost, was back-

calculated for each year. Calculating the linear distance from the gatepost to the latitude of the capelin distribution epicentre and then dividing by the mean migration ground speed (12.1 km day^{-1}) from Olafsdottir and Rose (2012).

All acoustic data were recorded from Simrad EK500 echosounders attached to hull mounted calibrated 38 kHz split-beam transducers. For consistency with previous analyses, S_a (area backscattering strength (dB re 1 (m^2 m^{-2}); MacLennan *et al.*, 2002) values of maturing capelin were converted into number of fish per 100 m of survey track using the target strength (TS (dB re 1 m^2); MacLennan *et al.*, 2002) equation used in the Icelandic surveys:

TS (dB) = 19.1 * L (cm) – 74.5 dB, L=length of fish (cm) (Vilhjálmsson,1994) (4.1)

Bottom depth was also recorded and used to split acoustic data into on shelf (< 200 m bottom depth) and offshore (> 200 m bottom depth) data. As the present study addressed migration of the mature part of the stock, 100 m survey track bins having > 50 % juvenile capelin, as delineated by mid-water trawling, were not used in the analyses (Olafsdottir and Rose, 2012). The acoustic surveys use a 2-stage adaptive design in which both survey grid and boundaries are modified during the survey depending on capelin distribution and weather. The general pattern entails transects running east to west over the continental shelf edge, usually spaced 30 to 50 km apart (Fig. 3.3). To facilitate comparison between years when calculating the date of capelin presence on the migration route the distance from latitude 63 – 67 °N was divided into ten equally sized bins of 0.4 °N or approximately 50 km. When capelin were located within a latitude bin the average date

was calculated. The minor abundance of capelin (< 0.1 %) located on the continental shelf (< 200 m bottom depth) north of 65 °N was excluded from the analysis. All average calculations of distribution and dates were weighted by capelin abundance.

4.3.2 Biological sampling

Biological sampling was conducted, four to 75 samples per year (Table 4.1) using a pelagic trawl with 9 – 42 mm mesh in the cod end. One hundred haphazard selected capelin were measured for length, weight, sex, maturity and roe weight from each fishing set. Capelin were considered to be maturing that year if gonads were developing by January 1st (Vilhjálmsson, 1994). Only female gonads were weighed as weight changes in male gonads are much smaller (Vilhjálmsson, 1994). Capelin maturity was quantified as roe content:

$$\text{Roe content (\%)} = (\text{roe weight (g)} / \text{total fish weight (g)}) * 100 \qquad (4.2)$$

Capelin males are significantly larger than females (Vilhjálmsson, 1994), hence, fish size was calculated by sex. Immature fish were excluded from average roe content and size calculations. All samples were included in the calculations but were weighted by capelin abundance.

4.3.3 Temperature

Sea surface temperature (SST) was assumed to be an appropriate proxy for ambient temperature as capelin feed during summer and fall in the surface layer (< 50 m; Vilhjálmsson, 1994). In the fall, reduced surface warming and increased vertical mixing causes a uniform temperature profile in the epipelagic layer (< 200m; Kara *et al.*, 2003; Jónsson and Valdimarsson, 2005; Jónsson, 2007) Maturing capelin migrate almost exclusively within the epipelagic zone (Olafsdottir and Rose, 2012). SST was derived from monthly optimum interpolation (OI) data, based on advanced very high resolution radiometer satellite data, version 2 (NOAA_OI_SST_V2). These data have a spatial resolution of 1° latitude/longitude, temporal resolution of a month and represent the top 0.5 m of the ocean surface (Xue *et al.*, 2003) and were provided by the NOAA/OAR/ESRL PSD, Boulder, Colorado, USA, from their web site at http://www.esrl.noaa.gov/psd/. The average monthly SST from August to December for the historical summer and fall feeding grounds of capelin (67° - 71° N; Fig. 4.1; Vilhjálmsson, 1994, 2002) was calculated and summed into one value for each year (Tempsum).

4.4 Results

4.4.1 The spawning migration cue

The average date that acoustic surveys encountered capelin (50% of spawning stock biomass) on the eastern spawning migration route, south of 67 °N, ranged from January 8th (day-of-year (DOY) 8.3) to 26th (DOY 25.5) for the 12 spawning cohorts investigated

between 1992 and 2007 (excluding 1994, 1996, 1997 and 2005) (Fig. 4.2). Average date of encounter was not correlated to beginning date of surveying (correlation coefficient = 0.46, $p = 0.128$). Capelin distribution epicenters (centroid) ranged from latitude 64.4 to 66.5 °N, a difference of approximately 250 km. The average date of capelin encounter and epicenter latitude were not correlated (correlation coefficient = 0.28, $p = 0.371$), indicating that spawning cohorts encountered later in the year were not located significantly further south (lower latitude) once survey date was taken into account.

The annual capelin spawning migration passed the 67 °N gatepost on their way south from December 23rd (DOY 22.8) to January 20th (DOY 19.9) between 1992 and 2007, based on the back-calculated date of passage by half the spawning migration (Table 4.1).

Four explanatory variables were investigated as possible migration timing cues for the offshore phase: Tempsum, SSB, fish length and roe content. Integrated monthly mean temperatures (Tempsum) from August to December (including both months) on the capelin feeding grounds, 67 – 71 °N (Fig. 4.1) ranged widely from 14.5 to 24.7 °C (Fig. 4.3a). Temperature increased near monotonically from 1993 to 2004, with 2004 being 70 % warmer than 1993. During the last two years of the study period, 2006 and 2007, temperature declined to 1995 – 1998 levels. Spawning stock biomass (SSB) back calculated to January 1st (Anon, 2010) fluctuated from 639 to 1485 thousand metric tons between years (Fig. 4.3b). Average total length of male capelin ranged from 15.6 to 17.1 cm (Fig. 4.3c) and average roe content of maturing females was 5.2 to 9.3 %. As expected, survey date affected capelin maturity as roe content was significantly higher when capelin were encountered at a later date ($F_{1,6} = 54.72$, $p < 0.001$; Fig. 4.4a). Hence,

roe maturity was eliminated as a potential cue. In contrast, the latitude of the capelin epicenter had no effect on roe content ($F_{1,6} = 1.29$, $p = 0.299$; Fig. 4.4b).

A multiple regression analysis showed that the migration epicentre crossed the gatepost latitude (67 °N) significantly earlier ($F_{3,8} = 4.89$, $p = 0.032$, $R^2 = 0.51$) when SSB was larger (Fig. 4.5a) and feeding ground temperatures (Tempsum) were colder (Fig. 4.5b). Tempsum and SSB explained similar amounts of the variance (Table 4.2).

4.4.2 Staging area on the eastern spawning migration route?

In the first week of January (DOY 1 to 7) the leading southern edge (not the epicenter) of the capelin spawning migration had progressed southward and reached latitude 64 °N for the 12 spawning cohorts investigated (Fig. 4.6a). Capelin did not migrate inshore (< 200 m bottom depth) until the sixth week of the year (DOY 36 to 42; Fig. 4.6a – h).

Capelin were present in offshore (> 200 m bottom depth) latitude bins on the eastern spawning migration route, 63.4 – 67.0 °N, from January 4th (DOY = 4) to March 2nd (DOY = 61) for the 12 spawning cohorts investigated (Fig. 4.7a). Duration of capelin passage through the offshore latitude bins was calculated as the difference in the earliest and the latest dates of occupancy. The earliest capelin encounter on the spawning migration route was on January 4th in latitude bins 64.4 to 64.8 °N in 1992. On this particular occasion, acoustic surveying was conducted in the opposite direction to the southward migrating capelin, with the southern edge of the migration encountered first. The southern edge of the spawning migration had obviously passed more northern latitudes earlier. Hence, for calculation of duration in offshore latitude bins the earliest date of occupancy was changed to January 4 (DOY 4) for latitudes bins north of 64.8 °N.

The duration of capelin presence in the offshore latitude bins ranged from 16 to 57 days (Fig. 4.7b). In latitude bins 64.0 to 65.6 °N duration was significantly greater than further north and south (T-test = 4.59; p = 0.002, df = 7). This area is subsequently referred to as the staging area (Fig. 4.8).

4.4.3 Staging exit cue mechanism

In years 1995, 1999, 2000 and 2006 included acoustic data located within the offshore (> 200 m bottom depth) area where migration was delayed prior to the inshore (< 200 m bottom depth) phase of the migration (survey 1) in addition to later data when the cross shelf phase of the migration had commenced (survey 2). These four years of data facilitated investigation of the staging exit cue.

Temperature in the staging area was estimated using daily sea surface temperatures on a 0.25 * 0.25 °latitude/longitude grid when capelin were present (Olafsdottir and Rose, 2012). The average ambient staging area temperature ranged from 2.4 to 6.9 °C for the eight surveys conducted in 1995 (Fig. 4.9a), 1999 (Fig. 4.9b), 2000 (Fig. 4.9c) and 2006 (Fig. 4.9d). Temperature differences between the offshore and shelf regions varied. Temperatures in the offshore staging area were significantly colder during survey 1 in 1995 and 2006 (Table 4.3), whereas in 1999 and 2000 temperatures were significantly colder during survey 2. There was no obvious relationship between temperature and the initiation of the final stage of the migration.

Average female roe content was calculated separately for capelin located in the offshore staging area and inshore during survey 2. If a biological sample was assigned to acoustic data recorded both inshore and in the staging area then the sample was only

allocated to the area with higher capelin abundance for that particular sample. In survey 1, capelin were only present within the offshore staging area. Average roe content ranged from 4.9 to 17.2 % for the eight surveys conducted in 1995 (Fig. 4.9e), 1999 (Fig. 4.9f), 2000 (Fig. 4.9g) and 2006 (Fig. 4.9h). In all four years, capelin that had ventured inshore were more mature than capelin located in the offshore staging area (Table 4.4). Capelin consistently migrated inshore from the offshore staging area when roe content surpassed 12 - 14 %. Male gonads were not weighted.

4.5 Discussion

4.5.1 Beginning of the spawning migration

The annual spawning migration of the Icelandic capelin stock that utilized the major eastern route varied in timing when capelin epicenter crossed the 67 °N gatepost within a month. Approximately 50% of the variability in timing was explained by spawning stock biomass (SSB) and feeding ground temperatures. In essence, larger SSB and colder temperatures correlated with an earlier migration. Surprisingly, neither average gonad maturity nor average fish length influenced initial migration timing. Temperature is the most important oceanographic factor influencing fish growth and maturation, hence, a negative relationship between temperature and the onset of migration is consistent with fish size and maturity having little effect on migration timing. This appears to be in contrast to other capelin stocks.

The Newfoundland capelin stock has been reported to migrate earlier when temperatures are warmer and fish larger (Shackell *et al.,* 1994; Carscadden *et al.*, 1997).

Shackell *et al.* (1994) suggested that temperatures influence capelin growth and gonad maturation, with fish growing and maturing at a faster rate in warmer years and subsequently migrating earlier.

The observed difference in spawning migration cues between the Icelandic and the Newfoundland stock is likely caused by ecological differences between these regions and stocks. The Newfoundland stock begins its spawning migration in spring (April - May; Shackell *et al.,* 1994) simultaneously with the onset of feeding (Winters, 1970) and increasing seasonal temperatures (Carscadden *et al.*, 1997). Newfoundland capelin typically spawn in June and July (Carscadden *et al.*, 1997). In contrast, the Icelandic stock begins its spawning migration in the middle of winter (December – January) when feeding is non-existent or very limited. Feeding and growth of Icelandic capelin is near nil in winter (Vilhjálmsson, 1994) and temperatures are decreasing (Jónsson, 2007). During winter, migrating Icelandic capelin convert somatic fat collected during the feeding season into gonad tissue en route (Vilhjálmsson, 1994). Hence, migrating pre-spawning capelin encounter very different situations in Iceland and Newfoundland, with declining temperatures in the former and the increasing temperatures in the latter. The Barents Sea capelin stock faces declining temperatures (Loeng, 1991) during their winter spawning migration and migrate several weeks earlier in colder years then during warm years (Ozhigin and Luka, 1984) similar to the Icelandic stock. It seems logical that warmer conditions in Newfoundland would accelerate maturation and lead to earlier spring migration, but in Iceland and the Barents Sea warming would lead to increased fall feeding opportunities and a delay in migration. These possibilities are consistent with the

data from the three stocks and demonstrate adaptation of the spawning migration to different temperature regimes.

Capelin distribution is sensitive to temperature changes (Rose, 2005), with increasing and decreasing temperatures capable of causing sudden distribution changes (Saemundsson, 1934; Frank *et al.*, 1996). During my study period, temperatures north of Iceland (66 - 71 °N) peaked in 2005 and have since declined (Jónsson and Valdimarsson, 2012; Fig. 4.3). Warmer temperatures coincided with shifts in fall distribution of maturing capelin from 2002 to the end of study in 2007 (Anon 2002-11; Pálsson and Björnsson, 2011). Historically in fall maturing capelin is located on the shelf edge northwest, north and northeast of Iceland during the years 2002 to 2007 (<68 °N; Vilhjálmsson, 1994, 2002). During these years temperatures were colder and capelin migration followed the major eastern route (< 67 °N) in the first half of January (Vilhjálmsson, 1994, 2002). In 2002, however, the fall distribution of capelin changed as pre-spawning fish were no longer located on the shelf edge (Anon, 2003 – 2008; Pálsson and Björnsson, 2011) and this situation has continued throughout the remainder of the present study until 2007. It is noteworthy that despite extensive searching efforts in the fall to locate the spawning cohorts in these years, they were not found before January when they entered the eastern spawning migration route. Despite this fall redistribution of pre-spawning adults during these years, the spawning migration route and spawning grounds remained unchanged (Olafsdottir and Rose, 2012). It was concluded that capelin had shifted their fall distribution further to the north (> 68 °N) or west to the shelf of Greenland in response to the warmer waters (Astthorsson *et al.*, 2007; Anon. 2002 - 2008). The observed shift displaced capelin considerably from their traditional fall

distribution and further away from the eastern spawning migration route (< 67 °N, > -14 °W). The greater distance between the fall distribution and the eastern migration route may help explain the later migration times observed from 2003 to 2007 and influence the negative relationship with temperature. It is worth mentioning that in the late 1970s and early 1980s pre-spawning capelin were located unusually far west in the Iceland-Greenland channel in the fall. These cohorts also entered the eastern spawning migration route in the latter half of January (Vilhjálmsson, 1994).

In recent years, from 2008 to 2011, capelin have returned to their traditional fall location on the shelf edge northwest, north and northeast of Iceland (Anon., 2008 – 2011). Unfortunately, these spawning cohorts were not included in the current study. Survey reports for the period do not record detailed locations or dates of the spawning migrations, hence, we do not know if capelin have been arriving earlier.

Capelin migrated earlier when stock size was larger. *In situ* results on the effects of stock size on fish migration timing are rare in the literature. One study on daily movements of pre-spawning herring on Georges Bank indicated that fish density had to rise above a specific threshold for the spawning migration to commence (Makris *et al.*, 2009). Capelin density peaks during the spawning migration but capelin begin to aggregate at increasing densities in the fall (October to December) (Vilhjálmsson, 1994) with the extent of the fall distribution area unrelated to stock size (Vilhjálmsson, 1994). Therefore, a larger spawning stock may reach higher density at an earlier date. It is possible that capelin, like herring, must reach a threshold density for the spawning migration to commence. To confirm the importance of density as the cue mechanism records of capelin density prior to the spawning migration are required. Analysis of

acoustic survey data collected in the fall was outside the scope of the current study. Nevertheless, it is an interesting question and worthy of further research.

4.5.2 Final phase of the spawning migration

My results indicate that Icelandic capelin using the eastern spawning migration route utilize an offshore staging area (> 200 m bottom depth) located at the southern end of the migration route prior to the final migration across the continental shelf to costal spawning grounds (Olafsdottir and Rose, 2012). The earliest recordings of capelin in the staging area occurred during the first week of the year (January 1 -7), but capelin were never located on the shelf (< 200 m bottom depth) and towards the south coast spawning areas in any numbers until week six (February 5 – 11). The staging phase lasted as long as five weeks. Staging location, and the extended delays of early arriving fish in the region suggest that staging evolved as a strategy to synchronize the final inshore phase of the migration to a specific time in early February (5 – 11; sixth week of the year). Records from spawning cohorts not included in the present study, 1979 to 1991 and 2008 to 2011, report the same results (Vilhjálmsson, 1994; Anon. 2008 – 2011). None of the 29 spawning cohorts recorded on the major eastern route between 1979 and 2011 entered inshore waters before early February despite the wide variance in the dates of arrival at the offshore staging area (Vilhjálmsson, 1994; Anon. 2008 – 2011).

Staging of fish in the open ocean has seldom been reported in the literature. In contrast, it is well documented that breeding migrations of birds commonly use staging areas to rest and replenish their energy reserves (Ebbing and Spaans, 1995). For capelin to have evolved a staging phase in their pre-spawning migration, life history theory

predicts there should be a fitness advantage. What possible advantage could accrue to capelin that wait offshore and delay the final inshore migration phase? They are not feeding (Vilhjálmsson, 1994). Fish do not require rest like airborne birds. The temperature difference between inshore and offshore locations was limited (see Figure 12a in Olafsdottir and Rose, 2012). I suggest that staging in capelin evolved to minimize cod predation, which is much more likely on the shelf where cod dominate the predator field for capelin.

The abundance of cod, the dominant predator of capelin, differs greatly between offshore and inshore areas (Vilhjálmsson, 2002). Cod distribution is limited to the continental shelf (< 500 m) and the majority inhabits the shallower coastal waters (< 200 m) (Begg and Marteinsdottir, 2002; Anon, 2011). Consequently, capelin are likely to incur much higher predation rates on the continental shelf than in the offshore region (Jaworski and Ragnarsson, 2006).

Capelin are the single most important prey for cod in Icelandic waters (Magnússon and Pálsson, 1989; Pálsson, 1997; Pálsson and Björnsson, 2011). In this region, cod are estimated to consume 350 to 900 thousand metric tons of capelin annually (Björnsson *et al.*, 1997). Approximately 70 % of the annual consumption occurs in winter (Pálsson and Björnsson, 2011) and consists mostly of pre-spawning capelin (Magnússon and Pálsson, 1991; Pálsson, 1997). The offshore spawning migration can take as long as five weeks (Fig. 4.6) and the inshore period is on average three weeks, hence, eight weeks in total. Let us consider a migration route over which the distribution of cod and capelin overlapped for eight weeks, as it could if capelin migrated directly south across the continental shelf towards the spawning area (Olafsdottir and Rose, 2012). Under this

scenario, cod could consume 150,000 to 400,000 metric tons of capelin in the extra five weeks migrating across the shelf (based on a weekly consumption of 30,000 to 80,000 tons; Björnsson *et al.*, 1997; Pálsson and Björnsson, 2011). Staging in the offshore, as demonstrated here, could reduce mortality of pre-spawning capelin by hundreds of thousands metric tons each year. It is likely no coincidence that staging occurs in an area that provides refuge from cod predation while being located immediately adjacent to suitable capelin spawning grounds.

Capelin exited the staging area and migrated towards the coast of southeastern Iceland after their gonads reached a specific maturity threshold. It appears that capelin use staging to synchronize gonad maturity to 12 – 14% roe content before migrating inshore. The average maturation rate of capelin roe inshore is 1% per day (Vilhjálmsson, 1994), hence, the duration of the inshore phase of the migration is 16 to 23 days as capelin spawn when roe contents is 30 – 35% of female total weight (Vilhjálmsson, 1994).

Timing of the inshore migration phase was not influenced by staging temperatures. In the staging area, two different ocean currents collide, the cold East Icelandic Current (1 – 3 °C) and the warm Irminger Current (5 – 8 °C) resulting in substantial temperature variability (Perkins *et al.*, 1998). The area has limited seasonal variation as temperatures are almost always within the range frequently occupied by pre-spawning capelin (Thors, 1981). Unpredictable temperature fluctuations on short temporal scales and no seasonal signal may limit the usefulness of temperature as an inshore migration cue.

In summary, the long distance (500 – 1000 km) eastern spawning migration route of the Icelandic capelin stock consists of these phases: offshore, staging, and inshore. Timing of the initial offshore phase varies up to a month whereas timing of the final inshore phase is relatively constant, with variable residence time at the staging area. The migration cues for the initiation of offshore and inshore movements appear to differ. Extrinsic factors associated with offshore timing. Capelin migrated earlier when spawning stock biomass was larger and feeding temperatures colder. Timing of the inshore phase appeared to be controlled by an intrinsic factor. A specific threshold in gonad maturity had to be surpassed before capelin migrated inshore. Cue mechanisms of the two different phases were not synchronized in most years. If capelin entered the offshore phase early, they reached the staging area well before gonad maturity advanced to required levels. In those years capelin staged offshore for extended periods as their gonads matured. The offshore location of the staging area provided a refuge from predation, with the maturation threshold limiting exposure to Atlantic cod to approximately three weeks.

4.6 Acknowledgements

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4.8 Tables

Table 4.1. The date when acoustic surveying began on the eastern migration route, south of latitude 67 °N, and the back calculated date when half the migration crossed latitude 67 °N, for 12 spawning cohorts. Numbers of biological samples used also included. Jan = January and Dec. = December.

Year	Date surveying began	Date crossed 67 °N	Biological samples (n)
1992	Jan. 4	Dec. 23	12
1993	Jan. 6	Dec. 24	12
1995	Jan. 4	Dec. 30	75
1998	Jan. 22	Jan. 7	4
1999	Jan. 15	Jan. 2	71
2000	Jan. 19	Dec. 29	40
2001	Jan. 15	Dec. 30	11
2002	Jan. 11	Dec. 29	21
2003	Jan. 9	Jan. 9	31
2004	Jan. 7	Jan. 15	32
2006	Jan. 3	Jan. 18	24
2007	Jan. 8	Jan. 20	22

Table 4.2. Multiple regression results for the effects of capelin male length, spawning stock biomass (SSB) and feeding ground temperatures (Tempsum) on the date when migration epicentre crossed the eastern spawning migration route gatepost (latitude 67 °N) for 12 spawning cohorts investigated. None of the interaction terms were significant ($p > 0.05$) and were eliminated from model. SS is the adjusted (type 3) sum of squares.

Source	Coefficient	SS	$F_{1,8}$	p - value
constant	60.22	21.84	0.50	0.501
capelin length	-4.19	29.01	0.66	0.440
SSB	-0.03	305.45	7.96	0.022
Tempsum	2.51	363.02	8.24	0.021

Table 4.3. Comparison of average staging temperatures before and after the inshore (< 200 m bottom depth) phase of the migration commenced in 1995, 1999, 2000 and 2006. One-tail t-test testing to determine if temperatures were colder before capelin migrated inshore.

Year	t_{df}	df	p-value
1995	-48.93	123	< 0.001
1999	18.43	58	>0.999
2000	30.41	57	>0.999
2006	-6.21	116	< 0.001

Table 4.4. Comparison of average gonad maturity of capelin located offshore (> 200 m bottom depth) versus inshore (< 200 m bottom depth) after the inshore phase of the migration commenced in 1995, 1999, 2000 and 2006. One-tail t-test testing if gonad maturity of capelin located offshore was less than maturity of capelin inshore.

Year	t_{df}	df	p-value
1995	-373.05	1024	< 0.001
1999	-892.64	1288	< 0.001
2000	-364.25	798	< 0.001
2006	-243.44	403	< 0.001

4.9 Figures

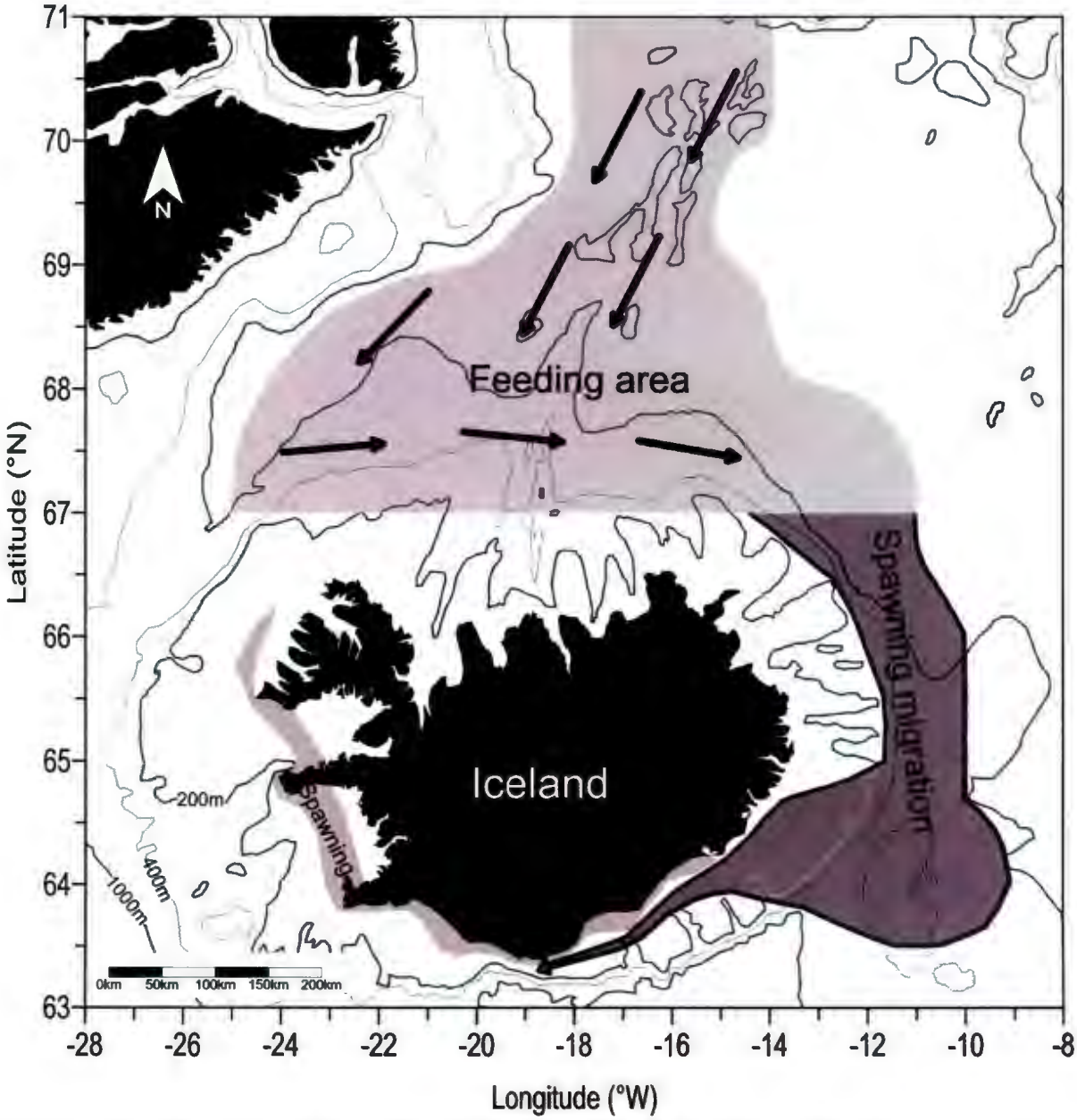


Figure 4.1. The study region, summer feeding areas and feeding migrations routes of maturing Icelandic capelin (solid arrows; drawn from fig. 3 in Vilhjálmsson, 2002). The dominant eastern capelin spawning migration route is also displayed (Olafsdottir and Rose, 2012) and their coastal spawning grounds (Vilhjálmsson, 1994).

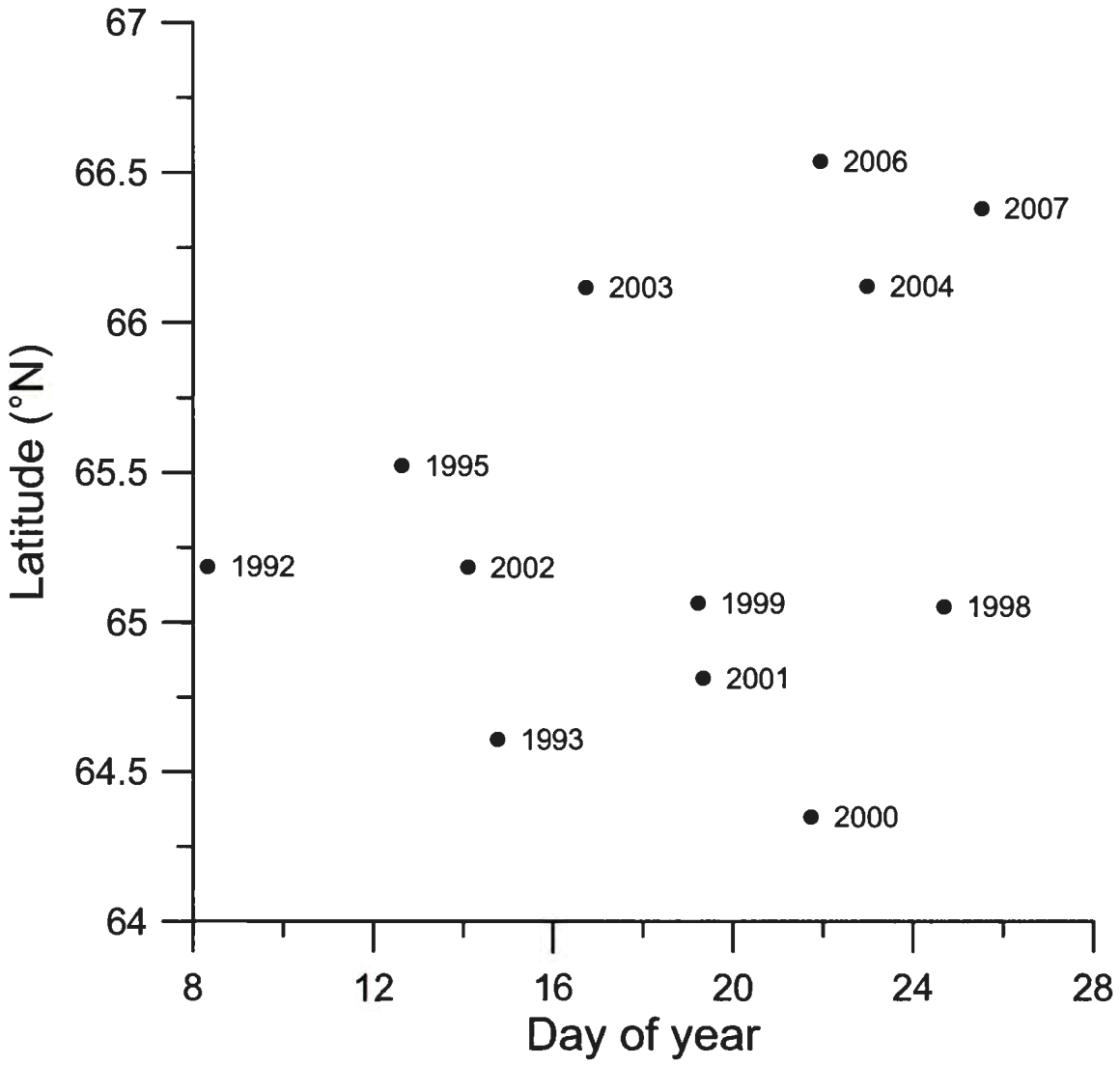


Figure 4.2. Average date (day of year; weighted by fish abundance) and epicentre latitude when the capelin spawning migration was first acoustically recorded on the eastern spawning migration route, south of 67 °N, for the 12 spawning cohorts investigated. Average day of year and epicentre latitude are not significantly correlated (correlation coefficient = 0.28, p = 0.371).

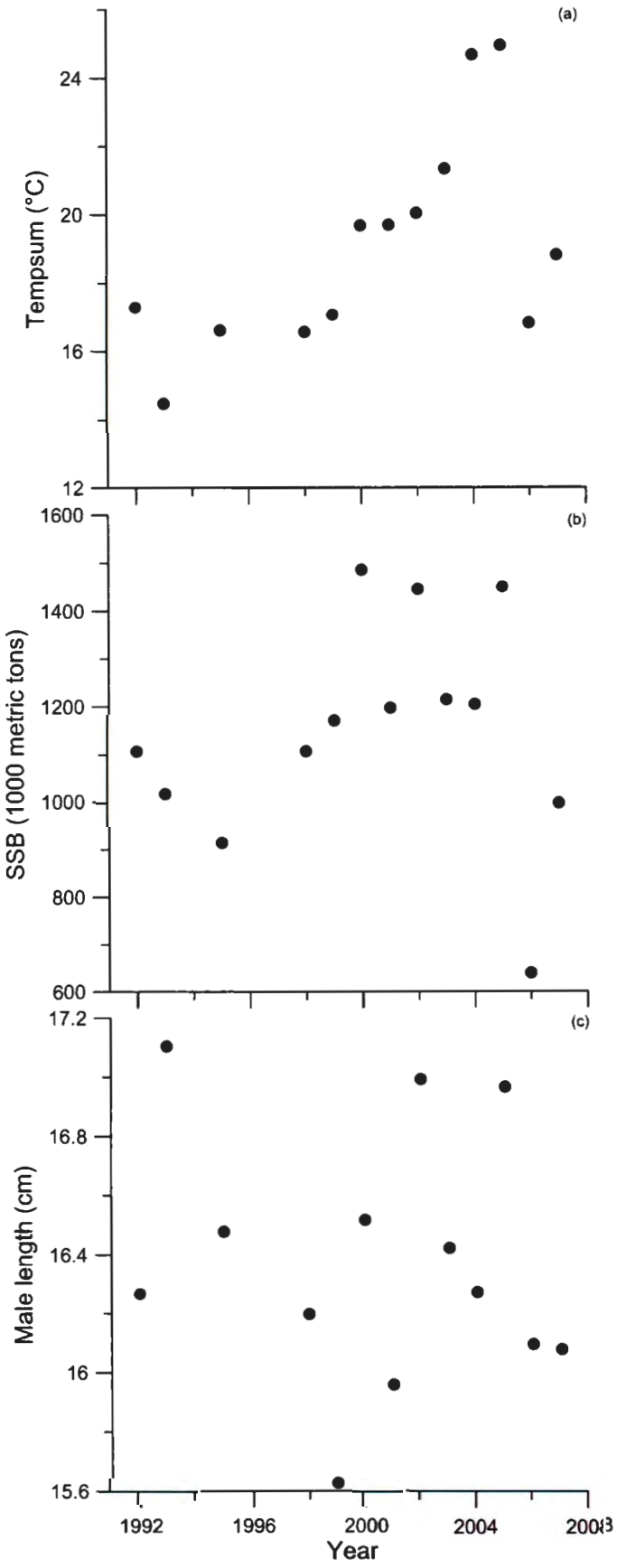

(a)
Tempsum (°C)
24
20
16
12
(b)
SSB (1000 metric tons)
1600
1400
1200
1000
800
600
(c)
Male length (cm)
17.2
16.8
16.4
16
15.6
1992
1996
2000
2004
2008
Year

Figure 4.3. (a) Integrated monthly mean temperatures (Tempsum) from August to December on the capelin feeding grounds (67 – 71 °N), (b) spawning stock biomass (SSB) back calculated to January 1 (Anon, 2010) and (c) average (weighted by fish abundance) total length of males, for the 13 spawning cohorts investigated between 1992 and 2007 (excluding 1994, 1996 and 1997). The 2005 cohort is included to display when Tempsum peaked.

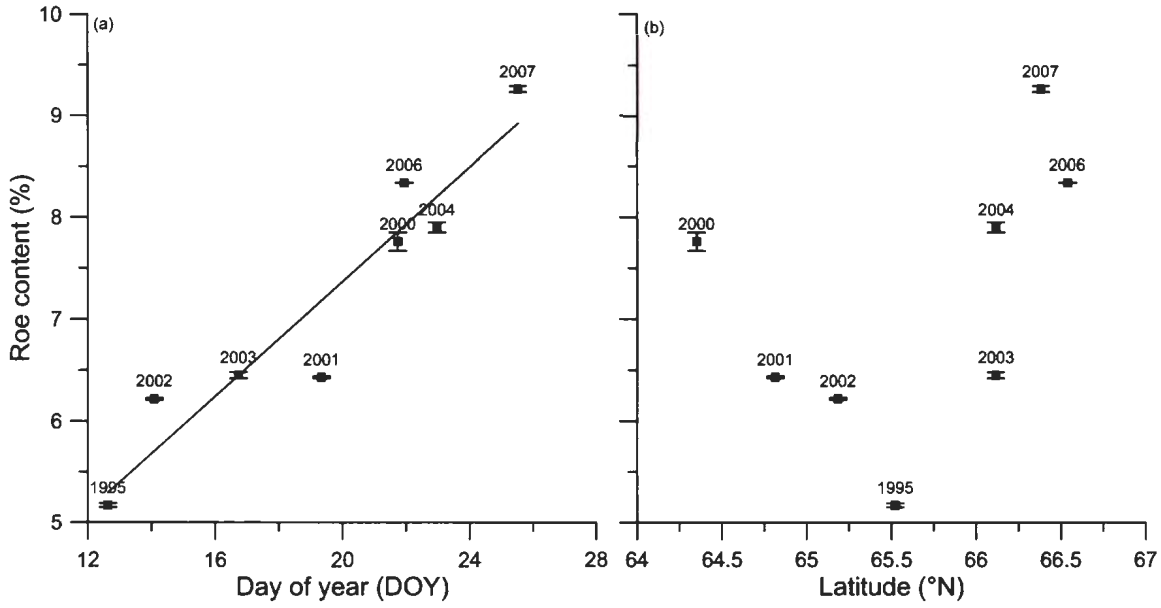


Figure 4.4. (a) Weighted (by fish abundance) average female roe content (%; ±95% confidence intervals) when the capelin spawning migration was first acoustically recorded on the eastern spawning migration route, south of 67 °N, for the 12 spawning cohorts investigated. (a) Roe content was significantly affected by survey date ($F_{1,6}$ = 54.72, $p < 0.001$); later encountered spawning cohorts were significantly more mature (roe content (%) = -3.66 + 3.20 * DOY, $r^2 = 0.90$). (b) Roe content (%; ±95% confidence intervals) was not affected by epicentre latitude (°N) (b; $F_{1,6} = 1.29$, $p = 0.299$). Immature fish were not included in roe content calculation. Ovaries were not measured in 1992, 1993, 1998 and 1999.

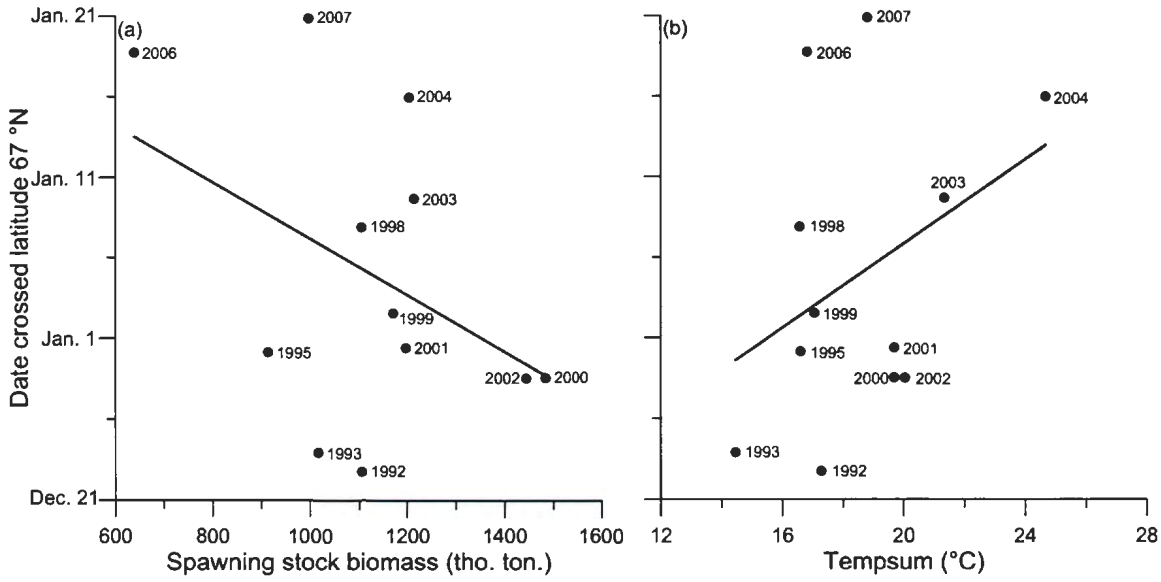
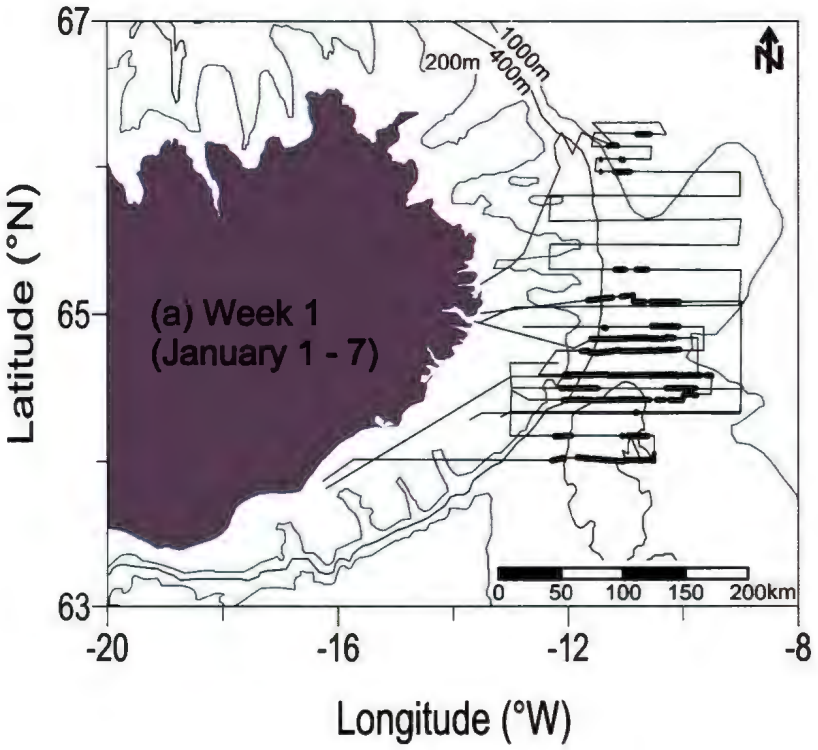
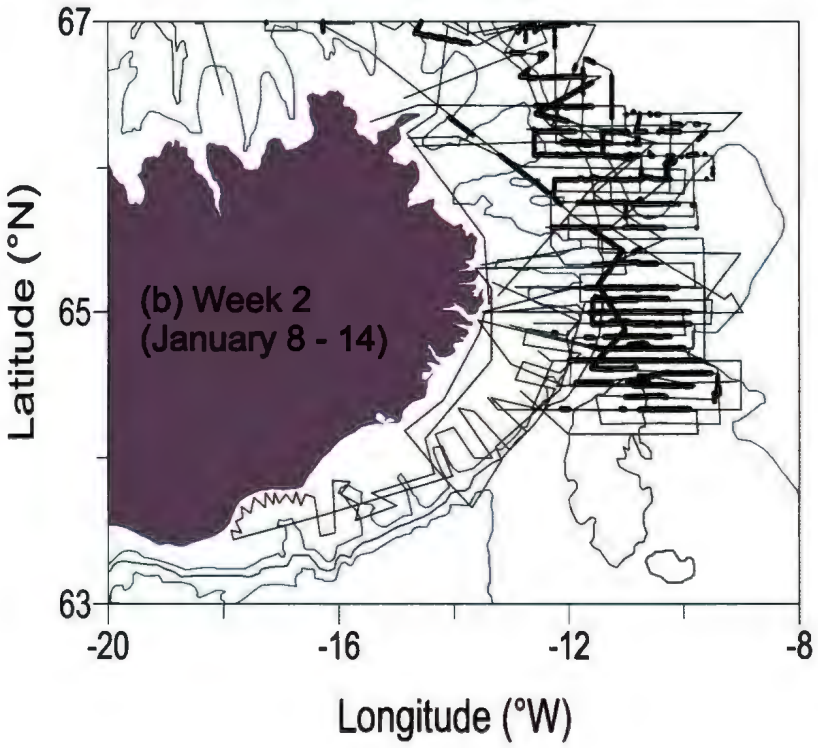
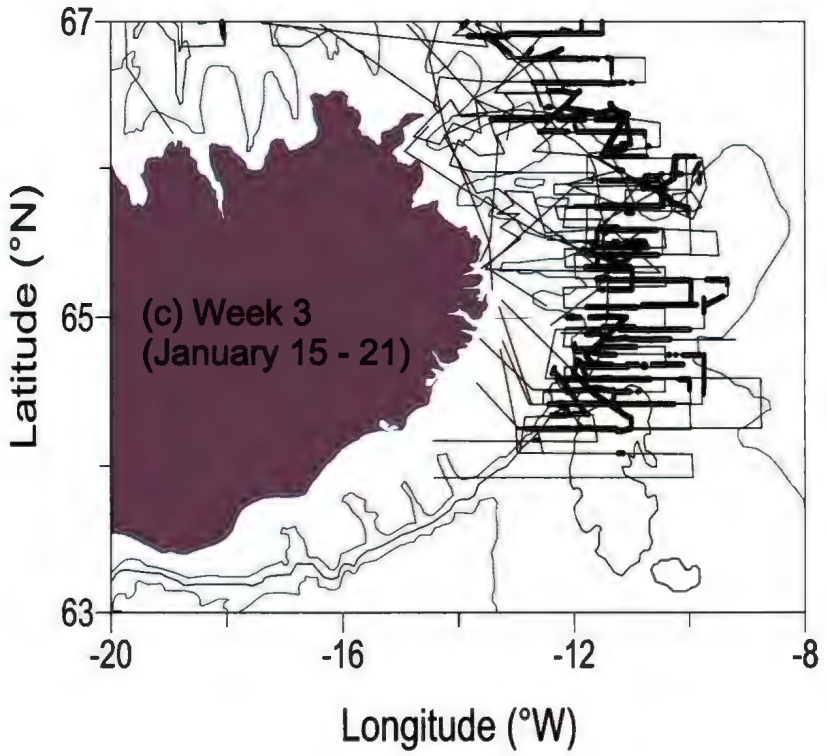
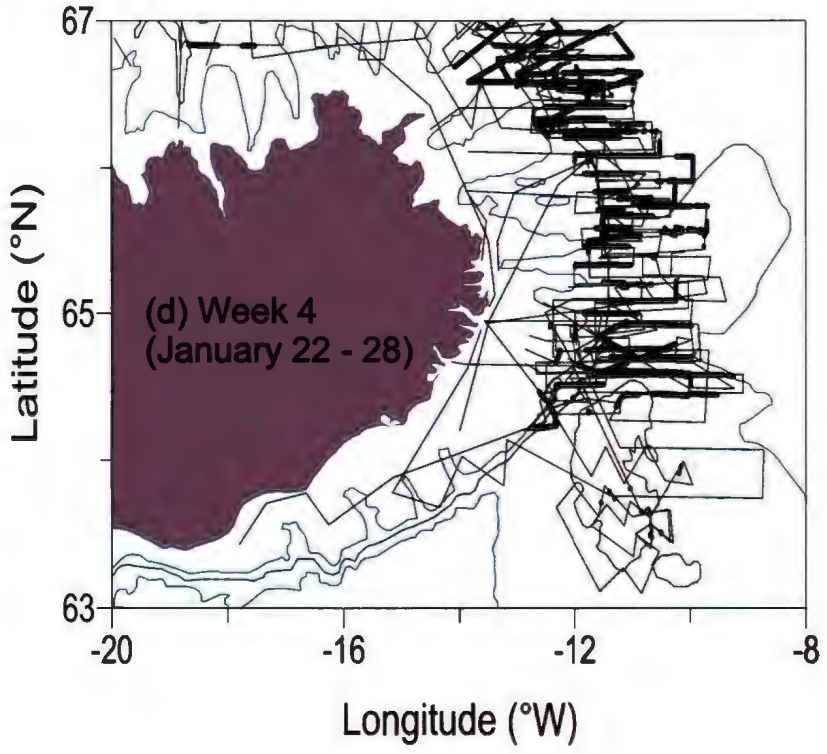


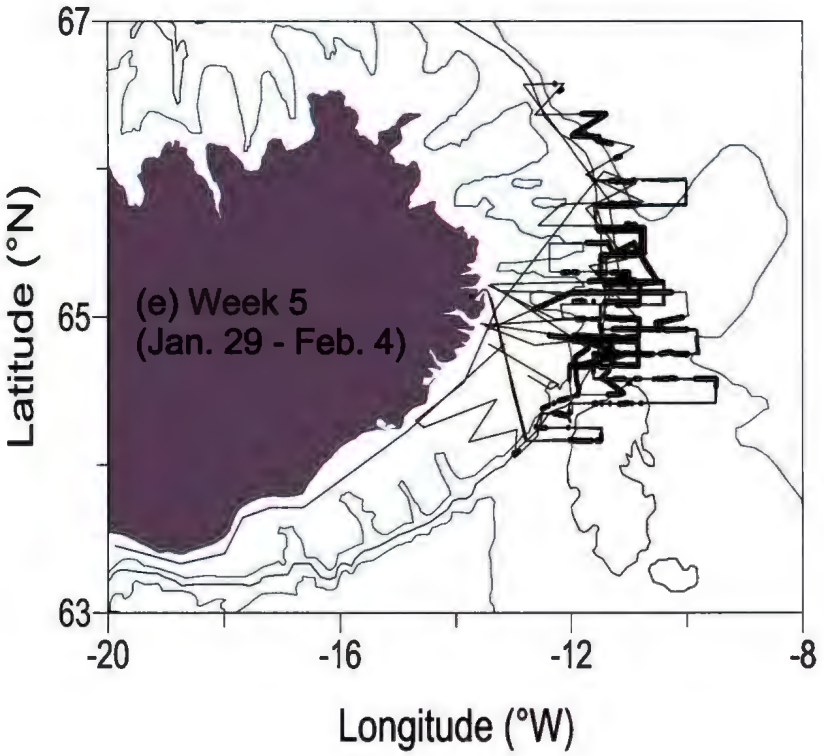
Figure 4.5. The epicentre of the annual spawning migration crossed the eastern spawning migration route gatepost (latitude 67 °N) significantly earlier (multiple regression: $F_{3,8} = 4.89$, $p = 0.032$; interactions not significant, $p > 0.05$, thus eliminated from model) in years when (a) spawning stock biomass (SSB; Anon, 2010) was larger and (b) integrated feeding ground temperatures (Tempsum) colder (migration date = -0.03 * SSB + 2.51 * Tempsum, $r^2 = 0.51$) for the 12 capelin spawning cohorts investigated.


67
65
63
-20
-16
-12
-8
Latitude (°N)
Longitude (°W)
200m
400m
1000m
(a) Week 1
(January 1 - 7)
0 50 100 150 200km


67
65
63
-20
-16
-12
-8
Latitude (°N)
Longitude (°W)
(b) Week 2
(January 8 - 14)


67
65
63
Latitude (°N)
(c) Week 3
(January 15 - 21)
-20
-16
-12
-8
Longitude (°W)


67
65
63
Latitude (°N)
(d) Week 4
(January 22 - 28)
-20
-16
-12
-8
Longitude (°W)


67
65
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-20
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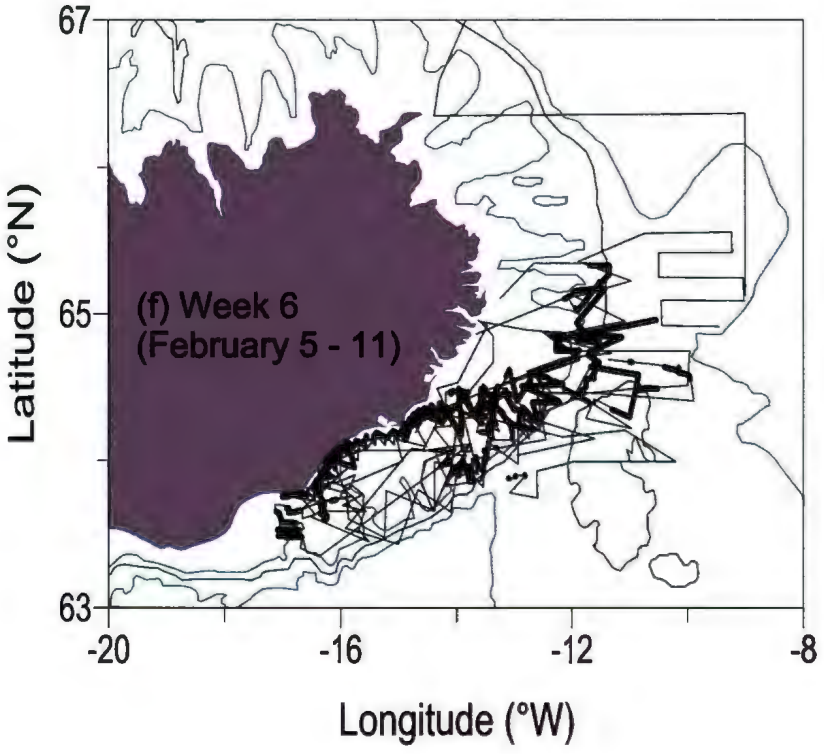
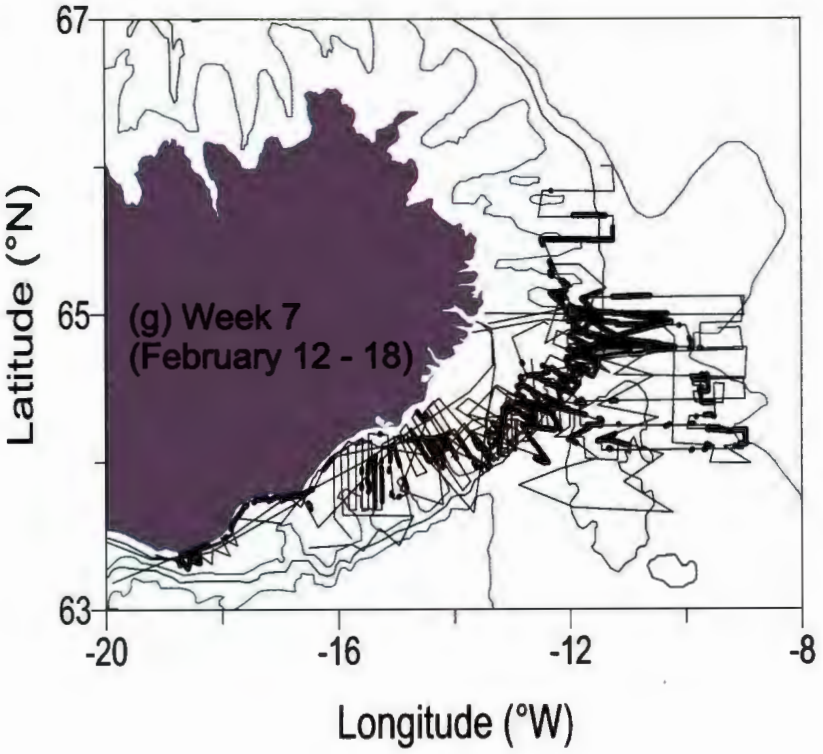
-12
-8
Latitude (°N)
Longitude (°W)
(e) Week 5
(Jan. 29 - Feb. 4)


67
65
63
-20
-16
-12
-8
Latitude (°N)
Longitude (°W)
(f) Week 6
(February 5 - 11)


67
65
63
Latitude (°N)
(g) Week 7
(February 12 - 18)
-20
-16
-12
-8
Longitude (°W)

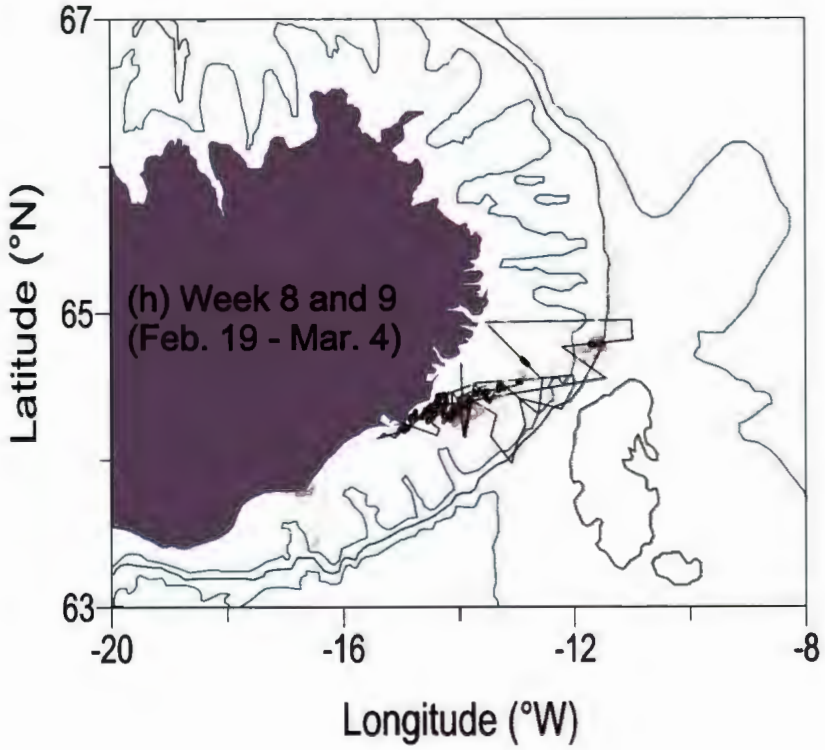

67
65
63
Latitude (°N)
(h) Week 8 and 9
(Feb. 19 - Mar. 4)
-20
-16
-12
-8
Longitude (°W)

Figure 4.6. Weekly capelin location (black and grey dots) on the eastern spawning migration route, south of latitude 67 °N, for the twelve capelin spawning cohorts investigated (a-h) and survey transects (black and grey lines). (h) Shows week eight (black) and nine (grey). Maps show capelin presence not abundance. Depth contours of 200, 400 and 1000 m are shown.

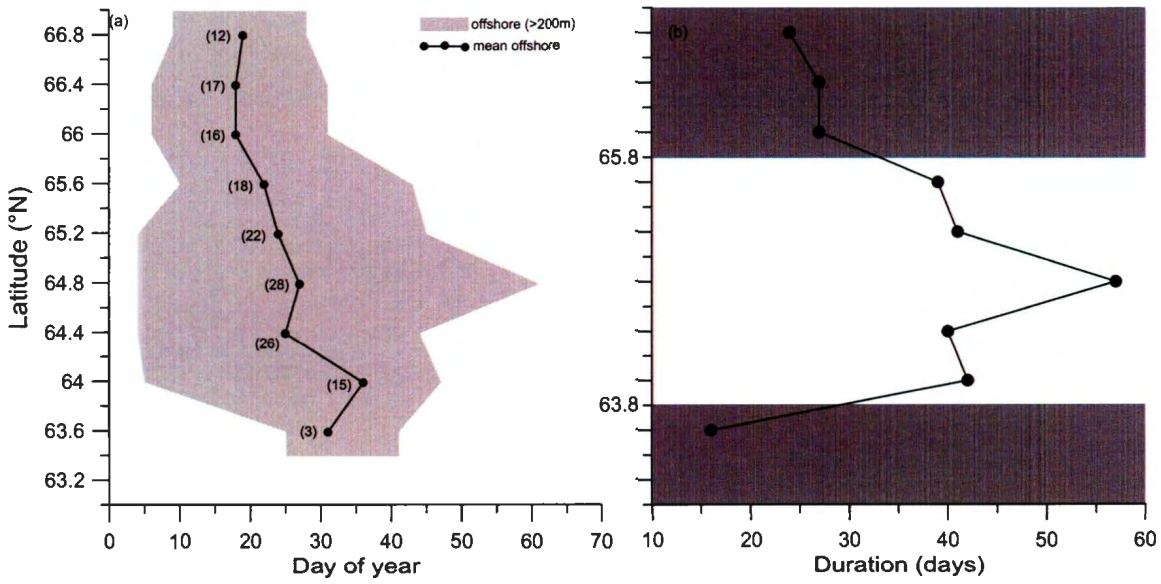


Figure 4.7. (a) Date range (grey) of capelin presence in offshore (> 200 m bottom depth) latitude bins (each 0.4 °N) on the eastern spawning migration route, south of 67 °N, for the 12 spawning cohorts investigated. Mean date per latitude bin reported (black line). Numbers of acoustic samples in offshore bins are displayed in brackets. (b) Duration of capelin presence in offshore latitude bins varied with latitude. The earliest date per latitude bin was changed to January 4th for all latitudes north of 65.2 °N when calculating capelin duration per latitude bin, see Materials and Methods. Duration of capelin presence was significantly longer in latitude bins 63.8 to 65.8 °N (non-shaded area) than further north and south (grey shaded areas) (T-test: $t = 4.59$, $p = 0.002$, $df = 7$).

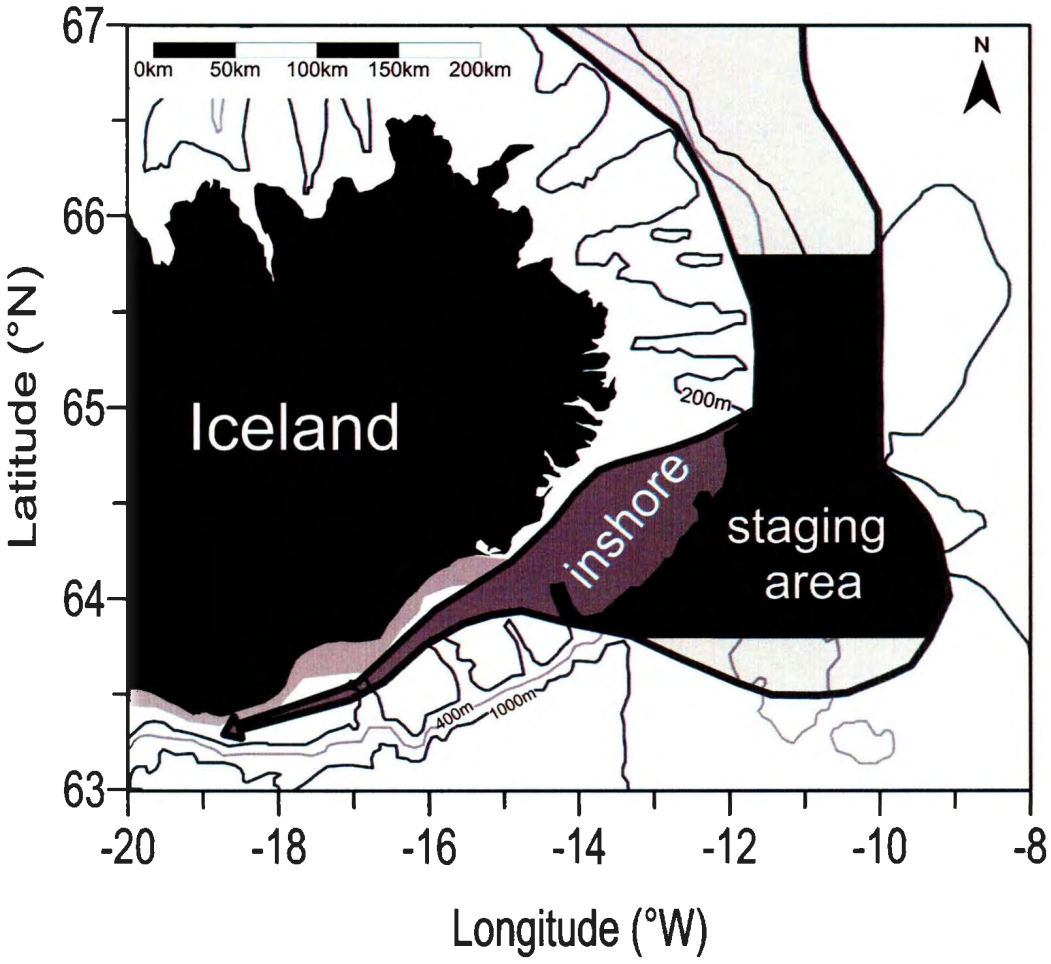


Figure 4.8. Location of an offshore (> 200 m bottom depth) staging area (black) utilized by maturing migratory capelin on the eastern spawning migration route for the 12 spawning cohorts investigate

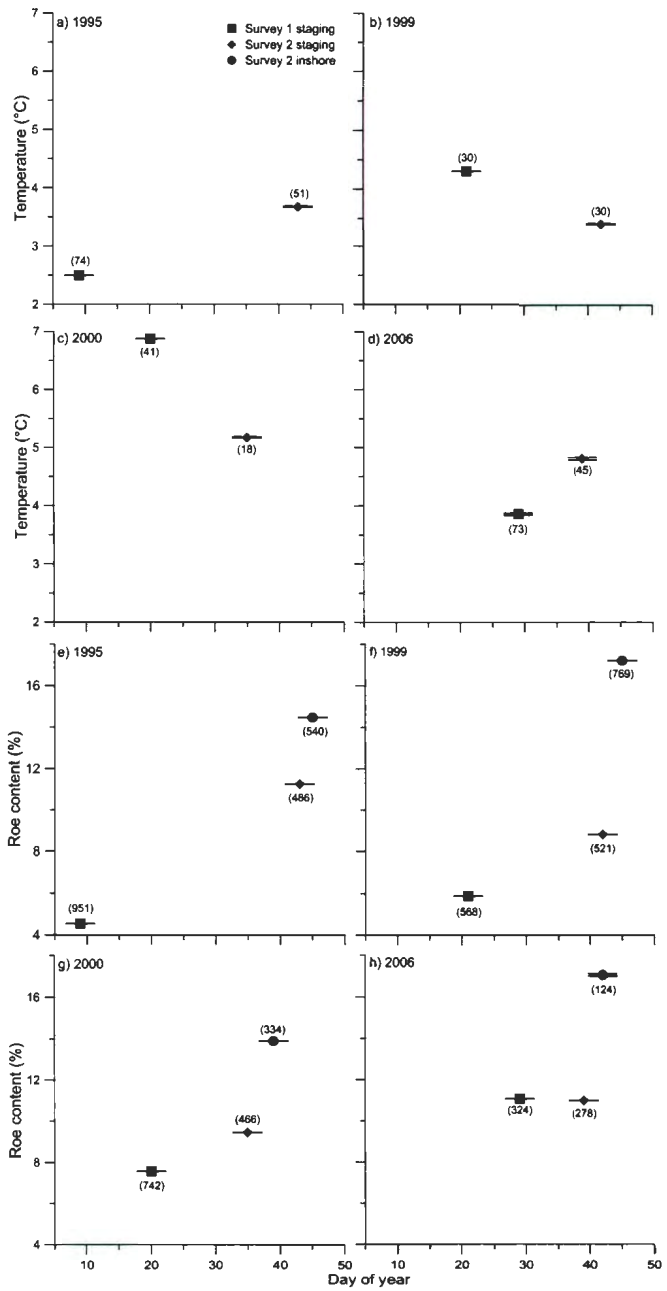


Figure 4.9. Average temperature (± 95 % confidence intervals, weighted by fish abundance) environment of capelin located within the staging area prior to inshore migration (survey 1) and later when inshore migration has commenced (survey 2) for years 1995 (a), 1999 (b), 2000 (c) and 2006 (d). Average female roe content (± 95 % confidence intervals, weighted by fish abundance) is displayed (e-h). Immature fish were not included in roe content calculations.

Chapter 5. Summary

This thesis reports the first comprehensive study on the spawning migration routes and migration timing of the Icelandic capelin stock. My research showed how bottom topography, temperatures, stock abundance and gonad maturity influence migration route and timing and use of staging area, based on 13 years of data.

Capelin is one of the most important fish species found in Icelandic waters. They are considered to be a keystone species in the sub-arctic ecosystem – providing the main conduit of energy from zooplankton to higher tropic levels, including predatory fish, sea birds and marine mammals. Capelin abundance and distribution affects both growth and recruitment of several predators, in particular the Atlantic cod, whales and sea birds.

Capelin are also commercially important. In years when the stock is large it is one of the most valuable Icelandic fisheries with an annual export value measured in hundreds of millions of dollars. The fishery focuses on pre-spawning fish caught during the spawning migration. The management policy is to protect 400 000 metric tons of maturing capelin, as determined by acoustic surveys, with any surplus available for harvest. Capelin recruitment to the spawning stock is highly variable and spawning stock biomass (SSB) is estimated every year before the fishery opens. Since the 1970s, capelin SSB has been measured annually using acoustic methods. In most years, abundance is measured during the spawning migration from early January to early March. Variable migration timing causes the survey period to be extended in some years as the commercial importance of capelin requires surveying to continue until the spawning migration has been located and measured.

Icelandic capelin feed in the cold (1 – 3 °C) deep (> 500 m bottom depth) waters of the Iceland Sea (67 – 72 °N) during summer and migrate southward (63 – 65 °N) to spawn in warmer (5 – 7 °C) coastal (< 100 m bottom depth) waters south and southwest of Iceland in winter (late February to early April). Since research began in the 1970s, the spawning migration was thought to utilize one major migration route along the east coast of Iceland. In some years, capelin utilized a shorter migration route along the west coast. Local knowledge suggests that since the 1930s, capelin have utilized the south and west coast spawning areas. Historical records, however, report a major shift in spawning migration routes and spawning grounds in the 1920s and 1930s. During that period, warmer Atlantic waters were injected onto the shelf north of Iceland and capelin spawning grounds shifted there. Consequently, the spawning migration routes of pre-spawning fish shifted to the north coast. Various models predict climate change might increase sub-arctic sea temperatures including those on the Iceland shelf. It is important to understand how various intrinsic and extrinsic factors influence the migration routes used and the location of their spawning grounds. Capelin is key stone species in the food web and any shift is distribution will affect breeding success and abundance of their predators.

Capelin is a prime candidate for acoustic surveying as they have a relatively large swim bladder and migrate in dense mono-specific schools in the pelagic zone. Acoustic recordings provide continuous records of horizontal and vertical location of capelin. Sequential surveying of moving schools enables estimation of abundance, distribution, behaviour and migration speeds. In this thesis, I analyzed acoustic recordings from the capelin winter acoustic assessment surveys of the Marine Research Institute, Reykjavik,

Iceland. In total, spawning migrations of 13 capelin cohorts were collected from 1992 to 2007, excluding 1994, 1996 and 1997.

My research demonstrated how spawning migrations of the Icelandic capelin stock utilized a major eastern route and a minor western route. The major route was influenced by an interaction between topography and water temperatures. Capelin skirted the shelf edge but avoided crossing the shelf until temperatures warm enough for spawning had been encountered offshore. Nevertheless, temperature alone does not explain why capelin skirted the shelf edge in the first part of the migration, as similar temperatures occurred both shoreward and seaward of the selected route, or why they abruptly veered inshore when warmer waters were encountered. Moreover, skirting the shelf edge requires a longer route to the spawning grounds than would be required by simply following the coast southward. Life history theory predicts there should be a fitness advantage to this longer route for it to have persisted. I suggest that cod predation, which is limited to the shelf, may have caused pre-spawning capelin to delay entering the shelf as long as possible. Predator avoidance could have facilitated the evolution of a two staged process used by pre-spawning capelin to search for suitable spawning grounds: first, capelin search for warm spawning temperatures offshore where their gonads mature, then seek out shallow waters for spawning. This process could explain how the observed shift in spawning location of capelin to the north coast of Iceland in the 1920s and 1930s came about. During that period, temperatures on the shelf north of Iceland were several degrees warmer than usual (4 – 5 °C) and warm enough for capelin to spawn. The proposed two stage process would have guided pre-spawning capelin to spawn on the north coast under the conditions present in the 1920s to 1930s. Temperatures north of

Iceland have been increasing in the last decades but have not reached spawning temperatures for capelin yet. If temperatures keep increasing and capelin spawning shift to the north coast the whole ecosystem on the Iceland shelf could be affected. Predatory fish and marine birds will either suffer food shortages or have to shift themselves. Cod distribution did shift north during the 1920s and 1930s and is likely to do so again.

The minor western migration route was used by the bulk of the spawning cohort in only one of the 13 years and by a small fraction of fish in several other years. How capelin choose between the eastern versus western migration route, was beyond the scope of my study. Nevertheless, differences in oceanographic conditions between eastern and western Icelandic waters may cause most capelin to select the eastern route. The east coast is dominated by one current creating uniform oceanographic conditions, within and between years, whereas a warm Atlantic current and cold Arctic water collide on the west coast causing a highly variable temperature condition within and between years. Temperatures create consistent guideposts on the eastern route but not on the west coast. Furthermore, the east coast current flows in the migration direction while the west coast has a countercurrent. I suggest the consistency of these thermal features and favorable current direction has led to the dominance of the eastern route.

My research also demonstrated how the cueing (beginning date) of the migration is correlated to SSB and temperatures as the annual spawning migration commenced earlier in years when SSB was larger and feeding ground temperatures were colder. Capelin migrated actively and although they may use consistent currents to facilitate migration they are not passive drifters. Furthermore, the migration was not continuous as capelin utilized a staging area located offshore but adjacent to the inshore spawning

grounds. Gonad maturity influenced staging duration as capelin surpassed a specific maturity threshold prior to migrating inshore. The staging area provided warm waters to stimulate gonad development in a location adjacent to potential spawning grounds. I suggest that staging may have evolved to reduce cod predation and increase the survival of capelin prior to spawning. While staging is well recorded in migratory birds it is not so for entirely marine fish. Hence, the reported staging of migratory capelin is a novelty.

Increased understanding of the factors that influence spawning migration routes of the Icelandic capelin stock will help predict if and how climate change could affect the ecosystems of Icelandic waters. Better understanding of migration timing helps with survey planning and could save expensive survey time. Fishing is the backbone of the Icelandic economy, hence, increased understanding of migration patterns and distribution of a keystone species like capelin is of great importance. If the migration routes change and spawning grounds shift to the north it would have detrimental effects on predatory fish, specifically Atlantic cod, on the south and west coast of Iceland. The continental shelf south and west of Iceland is the predominant fishing grounds for predatory fish today. Furthermore, the understanding gained on the spawning migration of the Icelandic capelin stock contributes to fisheries science on this species, which is of significant importance to the similar ecosystems in Newfoundland and Labrador waters and the Barents Sea. This thesis demonstrates how intriguing interactions between very different factors influence fish migration routes and timing.

In summarizing my thesis some limitations of approach are apparent. These limitations are a combination of the convoluted nature of the capelin spawning migration and data collection method. As previously mentioned, the majority of the data used in my

thesis was collected during the annual capelin assessment surveys. The goal of these surveys is to locate and measure abundance of capelin in the shortest amount of time for the commercial fishery to commence, and were not intended to support a study on migration. Nonetheless, the data proved valuable for several key questions that have been answered, but not all. One question that remains unanswered concerns the continuous migration cycle where fish move from nursing areas to feeding areas to spawning areas. There is no concrete definition of when or where the feeding migration ends and the spawning migration begins.

There were no data from the fall when capelin begin their maturation (November and December). Hence, capelin location and date when gonad maturation began remains unknown and could be used to define the beginning of the spawning migration. This caused problems in quantifying the spawning migration starting date. I decided to use a gatepost and average migration speed to calculate the date when maturing capelin passed through the gate. This method assumes migration speed and fall distribution of capelin to be constant between years. I suspect these assumptions may prove to be incorrect. If or how this might affect my conclusions about which factors influence migration initiation date remains unclear. To solve this definition dilemma a comprehensive study is needed of capelin distribution and migration during fall when maturation begins and feeding declines.

After utilizing the data at hand I do have several ideas for future research. Among them would be a test of the staging hypothesis by acoustically tracking the spawning migration and gonad development continually from when capelin enter the eastern migration route until the cross-shelf migration phase is completed by the whole stock.

Furthermore, capelin swimming speeds could be calculated and an attempt made to explain the variable ground migration speed observed. There is no doubt there are other related questions that could be addressed on this fascinating and important commercial species in the waters around Iceland, and indeed in other arctic-boreal regions of the North Atlantic and North Pacific Oceans.

APPENDIX I. Acoustic classification of macrophytes and juvenile gadoids in coastal Newfoundland.

I.I Abstract

Acoustic backscatter from shoals of juvenile gadoids (*Gadus spp*) and aquatic macrophytes, largely kelp (order *Laminariales*) was collected in Smith Sound, Newfoundland, Canada, from 3-25 m depth using a BioSonics DT-X echosounder (120 and 200 kHz). Frequency differences and predictive discriminant analyses (PDA) of energetic parameters of the backscatter were used to classify juvenile gadoids and macrophytes identified by visual (surface or underwater video camera) observation. Frequency responses did not differ; backscatter increased with frequency for both fish and macrophytes. An optimal PDA (highest classification success; 91%) used four of seven predictors measured: maximum volume backscatter, area backscattering coefficient, standard deviation of backscattering coefficient and mean volume backscatter, listed in order of importance. Backscatter was on average stronger and had greater variability from macrophytes than from juvenile gadoids. The optimal PDA correctly classified 86% of independent acoustic backscatter of juvenile gadoids and macrophytes. The PDA developed here may have widespread application to classifying kelp beds and juvenile gadoids, in coastal North Atlantic ecosystems.

Keywords: acoustics, coastal waters, juvenile gadoids, macrophytes, North-Atlantic, species identification.

I.II Introduction

Many aquatic macrophytes are known to scatter sound energy and acoustic methods have been used to record their presence and map their distribution (e.g. Maceina and Shireman, 1980; Thomas *et al.*, 1990; Sabol *et al.*, 2002). Most studies to date, however, have either known or assumed the source of the backscatter to be macrophytes. In both marine and freshwater seafloor ecosystems, macrophyte beds and adjacent areas are well known to be prime habitat for juvenile fish (Conrow *et al.*, 1990; Cote *et al.*, 2004; Sindilariu *et al.*, 2006); but few attempts have been made to separate their echoes.

Various methods have been developed for classification of acoustic targets. Empirical classification rules have been developed utilizing five categories of echo descriptors: positional, morphometric, energetic, environmental, and biological (Reid *et al.*, 2000), extracted either from acoustic signal of known identity or in the case of environmental and biological parameters, from ancillary data sampling. Classification schemes based on various combinations of echo descriptors and ancillary information have been used successfully to separat fish species in many different ecosystems (e.g. Rose and Leggett, 1988; Scalabrin *et al.*, 1996; Lawson *et al.*, 2001). In addition, zooplankton have been classified by species with varying degrees of success (Woodd-Walker *et al.*, 2003) and can be discriminated from pelagic fish (Barange, 1994). Frequency differences in echo amplitude have been used to classify species of zooplankton (Madureira *et al.*, 1993; Brierley *et al.*, 1998) and fish (Kang *et al.*, 2002). Overall, classification methods work best when separating species having different acoustic properties in simple ecosystems (Horne, 2000).

Coastal ecosystems in the Northwest Atlantic have relatively few fish species (Rose, 2007). Among the most numerous are resident juvenile gadoids (*Gadus spp*). After settlement, juvenile gadoids typically inhabit shallow coastal waters and by age two often aggregate into shoals (Rose, 2007) associated with coarse substrate, high bathymetric relief and macrophyte beds (Keats *et al.*, 1987; Cote *et al.*, 2004). These same waters are habitat for various species of macrophytes requiring solid substrate for attachment and light for photosynthesis (South, 1981).

Aquatic macrophytes exist at various densities and commonly form aggregations of several species (South, 1981). The acoustic impedance characteristics are not well known but backscattering strength has been shown to be related to biomass only at low density (Sabol *et al.*, 2002) and to increase with higher frequency, from 50 – 200 kHz (Shenderov, 1998). Fish backscatter, on the other hand, is well studied and known to be related to size, tilt angle and density (Simmonds and MacLennan, 2005). The frequency responses of juvenile gadoids are inconclusive and perhaps complex, as *ex situ* experiments by Rose and Porter (1996) showed slightly higher *TS* at 120 kHz than at 38 kHz for juvenile Atlantic cod (*Gadus morhua*) 18 – 40 cm in length, whereas *in situ* results from ICES (1994) for much smaller juveniles, 1.5 – 6 cm, showed higher *TS* at 38 kHz than at 120 kHz .

Since 1996, an acoustic monitoring program for Atlantic cod in coastal Newfoundland has revealed widespread macrophyte distribution in coastal waters (< 25 m). Several attempts to map their distribution and that of juvenile cod, using acoustic recordings, have been hampered by inabilities to reliably separate macrophytes from fish on echograms. Positional measures such as depth, location in the water column and

distance off bottom have been used to separate various fish echoes (Rose and Leggett, 1988; Lawson *et al,.* 2001) but were inadequate to separate macrophytes and juvenile fish because they occupy similar depths and locations. The goal of the present work was to develop an acoustic identification method, independent of positional parameters, which would distinguish juvenile gadoids from macrophyte backscatter.

I.III Materials and methods

I.III.I Study site and data collection

Smith Sound is a sheltered fjord, approximately 20 km long, 1.8 km wide and 350 m deep, located on the western side of Trinity Bay on the NE coast of Newfoundland, Canada (Fig. I.I). The Sound is a cold-water ecosystem with temperatures that range from 8 °C in late summer to subzero in spring (Smedbol and Wroblewski, 1997). There are relatively few resident fish species but after 1995 the Sound held the largest surviving group of over-wintering and spawning "northern" Atlantic cod (Rose, 2003), and also is home to rock cod (*Gadus ogac*) and cunners (*Tautogolabrus adspersus*). Juvenile gadoids are resident year-round in the shallower waters (25m) (Rose, 2007), often associated with various macrophyte species.

Acoustic data were collected in July and August 2007 and 2008 (Table I.I) using a calibrated (Foote *et al.*, 1987) BioSonics DT-X digital echosounder system (BioSonics Inc, 4027 Leary Way NW, Seattle, WA 98107, USA) with 120 kHz single beam (6°) and 200 kHz split-beam (6.5°) transducers, mounted in close proximity on the small (6 m) RV "Gecho". This vessel drew < 1 m of water and was able to survey very close to shore to

water depths less than the beam forming range of the transducers (approximately 3 m). Visual and camera observations indicated minimal boat avoidance behavior by juvenile gadoids at depths where they and macrophytes were abundant. Video recordings showed gadoids did not swim away when camera was submerged. The transducers transmitted alternately 0.4 ms pulses at the rate of 5 pulses s^{-1}, with an internal digitizing depth increment of approximately 1.4 cm. BioSonics Visual Acquisition™ software was used to store digitized data.

Acoustic data were collected at various locations within Smith Sound along irregularly spaced zig-zag transects running from the shoreline to a 25 m depth (Fig. I.I). For backscatter verification on August 22, 2007, an underwater video camera, Sea-Drop 950 (SeaViewer, 1212 N. 39th St., Suite 333, Tampa, FL 33605, USA, www.seaviewer.com) was deployed when backscatter became visible in the water column or changed abruptly and recordings were used to identify macrophytes and fish. During camera deployment, the boat was allowed to drift with engines off, causing variable survey speed, 0.06 - 3.0 m s^{-1}. Juvenile gadoids were at times distributed within the macrophyte beds, and account for some of the variability in macrophyte backscatter, but in most instances their echo traces were separated from those of macrophytes. Some fish likely avoided identification by the camera, but slow drifts in most cases allowed positive identification. Brown algae (order *Laminariales*) was the dominant macrophyte (South 1981). Fish observed were primarly juvenile Atlantic and rock cod and a few cunners. Auxiliary acoustic data were collected on three different dates in the same fjord using the same acoustic equipment and post-processing methods (Table I.I, Fig. I.I). All acoustic and video data presented in this paper were collected during daylight hours.

Echoview® 4.40 (Myriax Software Pty Ltd, Hobart, Tasmania, Australia) was used for analysis of the acoustic data. The position of the seafloor on all echograms was determined by experienced personnel and set manually. Variable survey speed caused different resolution of the survey track, hence, the echogram was split into horizontal intervals, ten or 50 meters (Table I.I), before integration. Note that the term "sample" in this manuscript has a special meaning and refers to an echo trace identified using the school module algorithms in Echoview®. A sample can be an individual or an aggregation of marine biota. Settings for the school module were established using preliminary empirical analyses (Reid *et al.*, 2000): minimum threshold of -60 dB, minimum school length of 1.00 m, school-height of 0.20 m, minimum candidate length 0.15 m, minimum candidate height 0.10 m, maximum horizontal linking-distance 2.00 m, and maximum vertical linking distance 0.20 m. Eight acoustic variables were calculated for each defined sample: area backscattering coefficient (s_a; MacLennan *et al.*, 2002), mean volume backscattering strength (mean S_v; MacLennan *et al.*, 2002), maximum volume backscattering strength (max S_v), area backscattering strength (S_a; MacLennan *et al.*, 2002), frequency difference in area backscattering strength ($\delta S_{a200\text{-}120}$; MacLennan *et al.*, 2002), standard deviation of area backscattering coefficients (st.dev. (s_a)), and skewness and kurtosis of area backscattering coefficients.

I.III.II Statistical analysis

Two different methods of separating macrophyte and fish backscatter were tested, the first being frequency response differences between 200 kHz and 120 kHz. Difference in area backscattering strength between 200 kHz and 120 kHz ($\delta S_{a200\text{-}120}$) were tested using

a paired Student's *t*-test (Zar, 1999), for each interval and each target species. There were 332 intervals with macrophytes and 191 with fish.

The second method separated echo traces using echo descriptors, of which four types were initially considered as discriminators: energetic, morphometric, positional and environmental. Predictive Discriminant Analysis (PDA) (Huberty and Olejnik, 2006) uses predictor parameters to establish a classification rule for criterion groups. The primary questions PDA can answer are: how accurately can group membership be predicted and is correct prediction better than obtainable by chance, and, if so, how much better? For measured samples, covariance matrices were heterogeneous between groups ($\chi^2_{28} = 1223.4$, $p < 0.00005$) supporting the use of a quadratic classification rule, which uses within group covariance instead of pooled covariance, for all PDA models. Equal prior probabilities of groups were used as we had no previous knowledge supporting unequal priors and sample size was similar between groups (Huberty and Olejnik, 2006).

The optimal PDA has the highest number of correctly classified samples using the lowest number of predictors (Huberty and Olejnik, 2006). Ordering of predictors with respect to their contribution to the classification was investigated by deleting one predictor at a time from the optimal PDF (Huberty and Olejnik, 2006). To test if correct classification was better than obtainable by chance alone a z-value was calculated:

$$z = (n_{jj} - e_j) / \sqrt{[e_j (n_j - e_j) / n_j)]} \qquad (6.1)$$

where n_{jj} is the number of correctly classified samples, n_j total number of samples, and e_j is correctly classified samples by chance alone (Huberty and Olejnik, 2006). If the

number of correctly classified samples using the rule was significantly better ($p < 0.05$) than expected by chance, the improvement was calculated which gives the proportional reduction in classification errors relative to chance alone:

$$I = (H_o - H_e) / (1 - H_e) \quad (6.2)$$

where H_o is the number of correctly classified samples and H_e is the number of correctly classified samples expected by chance alone (Huberty and Olejnik, 2006). Correlation of energetic parameters in the optimal PDA was investigated by calculating the correlation coefficient (Zar, 1999). To test the predictive power of the optimal PDA algorithm it was used to classify additional acoustic data with known targets: macrophytes and juvenile gadoids that had not been used to develop the optimal PDA algorithm. SYSTAT® 12 (Systat Software, Inc. 225 W Washington St., Suite 425, Chicago, IL 60606, USA, www.systat.com) was used for statistical analysis.

I.IV Results

Preliminary attempts to visually identify and separate juvenile gadoids and macrophytes by inspection of echograms proved difficult, as expected (Fig. I.II). In comparing frequency responses, S_a was significantly stronger at 200 kHz than at 120 kHz for both fish (paired *t*-test, $t = -4.47$, $p < 0.001$, $df = 190$) and macrophytes (paired *t*-test, $t = -13.28$, $p < 0.001$, $df = 331$) (Fig. I.III). For fish, S_a differences between frequencies ranged from -7.0 to 6.4 dB (74% of samples higher at 200 kHz), with mean (calculated in the linear domain) of 1.1 dB and median 0.8 dB. For macrophytes, S_a differences ranged

from -2.6 to 9.3 dB (82% of samples higher at 200 kHz), with mean of 2.2 dB and median 1.8 dB.

Initial comparisons employing morphometric parameters were of limited use because of serious bias in measurements resulting from variable survey speed necessary during data collection. As anticipated, preliminary analyses indicated that positional parameters had little discrimination potential as they showed limited variation between groups. Similarly for environmental variables, the shallow waters (< 25 m bottom depth) in which most of the overlap occurred, distributions of macrophytes and juvenile gadoids exhibited limited spatial variability in temperature and salinity during summer. These analyses were not pursued.

Correct predictions from PDAs using one parameter at a time ranged from 88% for s_a to 63% for $\delta S_{a200\text{-}120}$ (Table I.II). A PDA using all seven energy parameters, however, correctly predicted the identity of 86% of juvenile gadoid and macrophyte samples (Table I.III), indicating over-parameterization when using all seven parameters. The optimal PDA reduced the predictors to four and had a success rate of 91% (Table I.III), although this reduction disproportionately affected classification success with a 14% increase for juvenile gadoids but 3% decrease for macrophytes. The four parameters of the optimal PDA were: max S_v, log (s_a), log (st.dev.(s_a)), and mean S_v, listed in order of contribution. The optimal PDA resulted in 82% fewer errors than classification by chance alone (Table I.III). In general, in comparison to macrophytes, juvenile gadoids had weaker backscatter, both average and maximum, and less within-sample variance in backscatter strength (Fig. I.IV). All parameters in the optimal PDA were positively correlated (Table I.IV), hence the relatively small improvement in classification success

over the single parameter PDAs of 3 - 9%. Correlation of parameters was expected as they are mathematically connected (MacLennan *et al.*, 2002). Classification success declined by 1 - 3% with elimination of any single parameter from the optimal PDA with disproportionally more fish than macrophyte samples incorrectly classified (Table I.III). These results justify the use of the four correlated parameters of the optimal PDA.

The proportion of correctly classified samples dropped from 91 to 86% when the optimal PDA was used to classify additional macrophyte and juvenile gadoid acoustic data which were not used to develop the algorithm (Table I.V). The decrease was the same for macrophytes and juvenile gadoids.

I.V Discussion

Acoustic backscatter was greater at 200 kHz than 120 kHz by similar amounts for the majority of both fish and macrophytes samples limiting the usefulness of multi-frequency classification at these frequencies. For juvenile gadoids, the stronger backscatter at higher frequency observed here is consistent with the results of Rose and Porter (1996) but differs from those reported by ICES (1994). For macrophytes, stronger backscatter at higher frequency is in accordance with theory (Shenderov, 1998) but there is little supporting empirical data. It is possible that backscatter at lower frequencies (e.g. 38 kHz), as reported by ICES (1994), would assist in frequency separation, but the logistics of using the much larger 38 kHz transducer from a small boat required to do this work are difficult. Moreover, the longer beam forming range of lower frequencies limits shallow water use where much of the macrophyte beds and juvenile gadoids occur. A higher

frequency (400 – 1000 kHz), which was not available for the present work, might provide a more amenable choice to compare with the 120 – 200 kHz signals.

The goal of predictive discriminant analysis (PDA) is correct classification of all samples. In reality, the proportion of correctly classified samples needed for classification to be labelled a success is a judgement call of the researchers (Huberty and Olejnik, 2006). Comparison with other studies can help estimate the success of our classification scheme. To our knowledge, the only other study on acoustic classification between fish (Atlantic salmon, *Salmo salar*) and macrophytes (Nealson and Gregory, 2000) used a stationary horizontal split-beam echosounder, and based on single target characteristics, achieved a very high success rate of 97%. Single target methods, however, in which isolated targets must be separated by at least half the acoustic pulse length (here 30 cm) (Simmonds and MacLennan, 2005), are not applicable to the coastal environment studied here. Both macrophytes and juvenile gadoids in Smith Sound typically occur at much higher densities making single target detection at best highly variable. Overall, successful classification rates in studies using integrated backscatter along with positional, morphometric and environmental parameters have been highly variable, ranging from 57 – 95%, in classifying three groups of fish and zooplankton species (Rose and Leggett, 1988; Barange, 1994; Scalabrin *et al.*, 1996; Brierley *et al.*, 1998; Lawson *et al.*, 2001; Woodd-Walker *et al.*, 2003). Woodd-Walker *et al.*, (2003) reported an overall classification of 72.5% based solely on energetic parameters. Our overall classification rate of 91% is therefore considered to be a success for a PDA of integrated backscatter.

The high classification rate of macrophyte samples that were independent of the initial learning set indicated that macrophyte beds in Smith Sound share a common echo

signature, characterized by backscatter with high maximum values and spatial variability. The high maximum can be explained by most macrophytes having gas-filled structures or bladders (pneumatocycts) on blades, or hollow gas-filled stipes (South, 1981), with the plant tissue having a much weaker backscatter. In addition, underwater video observations showed that backscatter strength varied widely and patches were often composed of varying types macrophyte species (Dayton, 1985). Moreover, Shenderov (1998) indicated that macrophytes do not show linear relationships between geometrical shape, plant size and backscattering strength, and also that backscatter may not increase linearly with increasing density, which is consistent with the present results indicating a common average echo signature among macrophyte beds composed of different species at various densities. This type of acoustic response fundamentally differs from that of fishes.

The presence of juvenile gadoids or other fish within macrophyte beds is not expected to affect classification. Their presence will likely increase backscatter from macrophyte beds, and perhaps lead to higher measure variability, but with the classification rule based on stronger and more variable backscatter of macrophytes than juvenile gadoids, this is thought unlikely to lead to misclassification.

In conclusion, juvenile gadoids and macrophyte acoustic backscatter can be separated, classified and mapped with good success using a predictive discriminant analysis based solely on energetic parameters. The method developed in this paper, if not the specific classification algorithm, may have widespread application to macrophyte beds dominated by kelp species and inhabited by juvenile gadoids, as is common in the coastal ecosystems of the North Atlantic.

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I.VIII Tables

Table I.I. Number of samples (macrophytes or juvenile gadoids), verification method and application of acoustic data collected at various location and dates within Smith Sound. A sample is an echo trace identified by the school module algorithms in Echoview, see materials and methods for definition. The survey track was split into horizontal intervals before integration to compensate for variable survey speed (0.06 – 3.00 m s^{-1}).

Date	Macrophyte	Fish	PDA[a]	Target verification	Horizontal intervals (m)	Max depth (m)
12 July 2007	0	319*	Test	Sampling	10	25
16 July 2007	0	184**	Test	Sampling	10	25
22 Aug 2007[b]	343	297**	Train	Video	10	15
14 Aug 2008	318	0	Test	Sight	50	20

[a] Samples were used to train or test the predictive discriminant analysis algorithms.

[b] Samples used to investigate frequency differences.

* Spawning capelin.

** Juvenile gadoids (*Gadus* spp.).

Table I.II. Univariate predictive discriminant analyses (PDA) of all seven energy parameters. All observed classification results were better than expected by chance (chance = 0.5, $p < 0.002$), except macrophyte classification for $\delta S_{a200\text{-}120}$, in bold. Parameters with a skewed distribution were transformed (log_{10}) before analysis.

Energetic parameter	Transformed	Univariate PDA (correctly classified %)		
		Macro-phyte	Juvenile gadoids	Total[a]
Area backscattering coefficient (s_a)	Yes	92	85	88
Maximum volume backscatter (max S_v)	No	91	82	87
Mean volume backscatter (mean S_v)	No	85	77	82
Standard deviation of s_a (st.dev.(s_a))	Yes	89	77	83
Skewness of s_a	Yes	83	63	74
Kurtosis of s_a	Yes	88	59*	75
$\delta S_{a200\text{-}120}$	No	**51****	78	63

*$p = 0.002$.

**$p = 0.706$, not significant.

a = total percentage of correctly classified backscatter, macrophytes and gadoids.

Table I.III. Predictive discriminant analyses (PDA) results using different subsets of energy predictors. All PDFs correctly classified samples better than expected by chance (prior probabilities of group membership = 0.5, $p < 0.001$). Bold represents overall correct classification per PDA model.

	Predicted group			
True group	Macrophyte (N)	Juvenile gadoids (N)	Correct (%)	Improvement over chance (%)
(a) All seven energetic parameters				
Macrophyte	325	18	95	90
Juvenile gadoids	72	225	76	52
Total	397	243	**86**	72
(b) The optimal PDA. Energetic parameters: max S_v, $\log(s_a)$, $\log(\text{st.dev.}(s_a))$ and mean S_v				
Macrophyte	314	29	92	83
Juvenile gadoids	30	267	90	80
Total	343	296	**91**	82
(c) Energetic parameters: max S_v, $\log(s_a)$ and $\log(\text{st.dev.}(s_a))$				
Macrophyte	315	28	92	84
Juvenile gadoids	38	259	87	74
Total	353	287	**90**	79
(d) Energetic parameters: max S_v, $\log(s_a)$ and mean S_v				
Macrophyte	311	32	91	81
Juvenile gadoids	37	260	88	75

True group	Predicted group: Macrophyte (N)	Predicted group: Juvenile gadoids (N)	Correct (%)	Improvement over chance (%)
Total	348	292	**89**	78
(e) Energetic parameters: max S_v, log(st.dev.(s_a)) and mean S_v				
Macrophyte	312	31	91	82
Juvenile gadoids	37	260	88	75
Total	349	291	**89**	79
(f) Energetic parameters: log(s_a), log(st.dev.(s_a)) and mean S_v				
Macrophyte	313	30	91	83
Juvenile gadoids	44	253	85	70
Total	357	283	**88**	77

Table I.IV. Correlation coefficients for the four predictors of the optimal predictive discriminant analysis algorithm (all are significant; $p < 0.05$).

	max S_v	$\log(s_a)$	log(st.dev.)
$\log(s_a)$	0.90		
$\log(\text{st.dev.}(s_a))$	0.97	0.89	
mean S_v	0.91	0.87	0.98

Table I.V. Classification of additional acoustic data using the optimal predictive discriminant analysis (PDA) algorithm. Equation 3.1 was used to calculate the z-score and equation 3.2 to calculate improvement over chance. The PDA predicted classification results were better than expected by chance alone. P-value from a one-tail normal distribution (Zar, 1999).

	Predicted group			Classification better than chance alone		
True group	Macrophyte	Juvenile gadoids	Correct classification (%)	z - score	p- value	Improvement over chance (%)
Macrophyte	277	41	87	13.23	< 0.001	75
Juvenile gadoids	27	157	85	9.58	< 0.001	71
Total	304	198	86	16.34	< 0.001	73

I.IX Figures

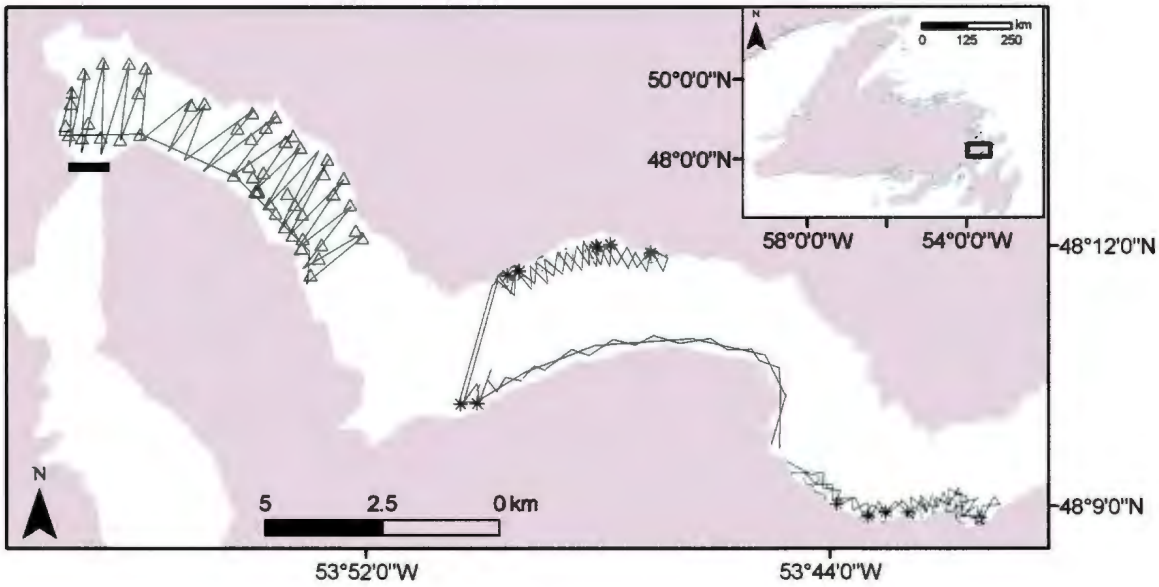

Figure I.I. Map of Smith Sound showing various sampling locations: 22 August 2007, juvenile gadoids (circle) and macrophytes (astericks) and survey transects (black line); 16 July 2007, juvenile gadoids (star); 12 July 2007, and 14 August 2008, macrophytes (triangle). Filled rectangle shows a causeway where Smith Sound becomes very shallow (< 1 m) and narrow (app. 20 m). Inserted map shows the location of Smith Sound (box) in Trinity Bay on the north coast of Newfoundland, Canada.

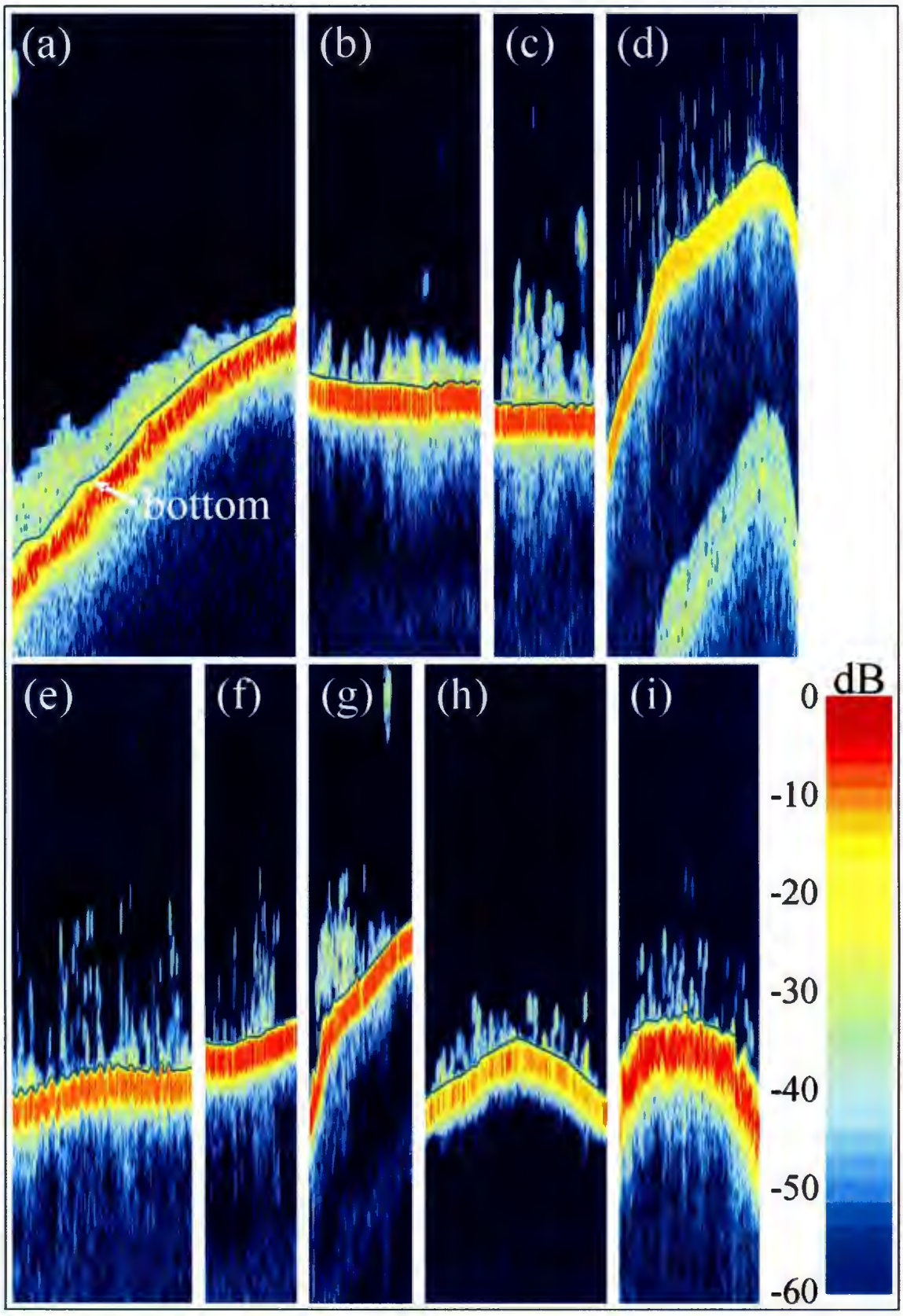
(a)
(b)
(c)
(d)
bottom
(e)
(f)
(g)
(h)
(i)
dB
0
-10
-20
-30
-40
-50
-60

Figure I.II. Echograms of juvenile gadoids and macrophytes from Smith Sound collected at 200 kHz: a) gadoid aggregation 38 m across and maximum height 1.9 m, bottom depth 13 – 17 m, survey speed 0.7 m s^{-1}; b) macrophyte aggregation 25 m across and maximum height 0.8 m, bottom depth 8.5 m, survey speed 0.4 m s^{-1}; c) macrophyte aggregation 20 m across and maximum height 2.5 m, bottom depth 9.0 m, survey speed 0.9 m s^{-1}; d) gadoid aggregation 57 m across and maximum height 1.8 m, bottom depth 3.0 – 5.5 m, survey speed 1.2 m s^{-1}; e) macrophyte aggregation 50 m across and maximum height 2.1 m, bottom depth 7 m, survey speed 1.3 m s^{-1}; f) macrophyte aggregation 58 m across and maximum height 2.1 m, bottom depth 9 m, survey speed 2.8 m s^{-1}; g) gadoid aggregation 40 m across and maximum height 1.7 m, bottom depth 7 - 9 m, survey speed 1.5 m s^{-1}; h) macrophyte aggregation 32 m across and maximum height 0.9 m, bottom depth 8 m, survey speed 0.8 m s^{-1}; i) gadoid aggregation 60 m across and maximum height 1.4 m, bottom depth 11.5 m, survey speed 2.0 m s^{-1}.

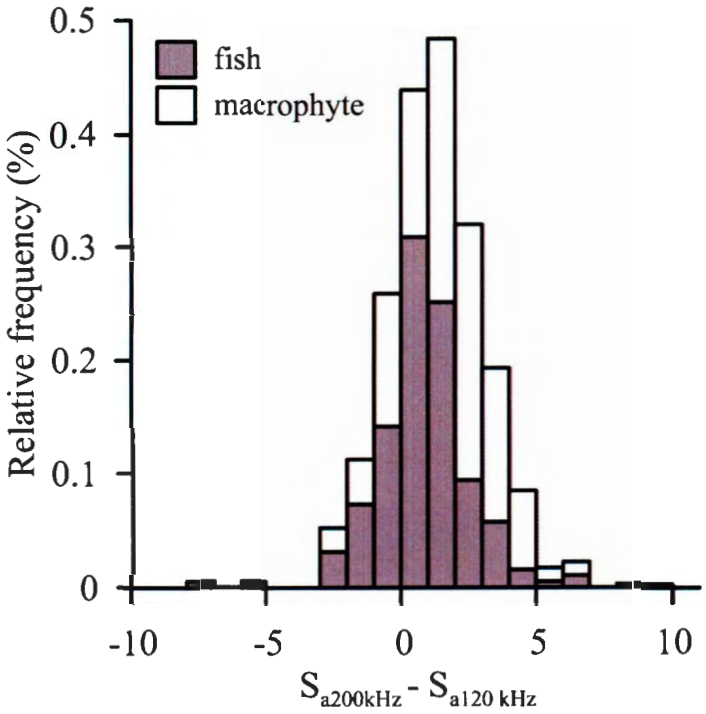

Figure I.III. Difference in backscatter strength between the two frequencies, 200kHz and 120 kHz, for macrophytes (open bars, n=332) and juvenile gadoids (filled bars, n=191), stratified into 1 dB intervals.

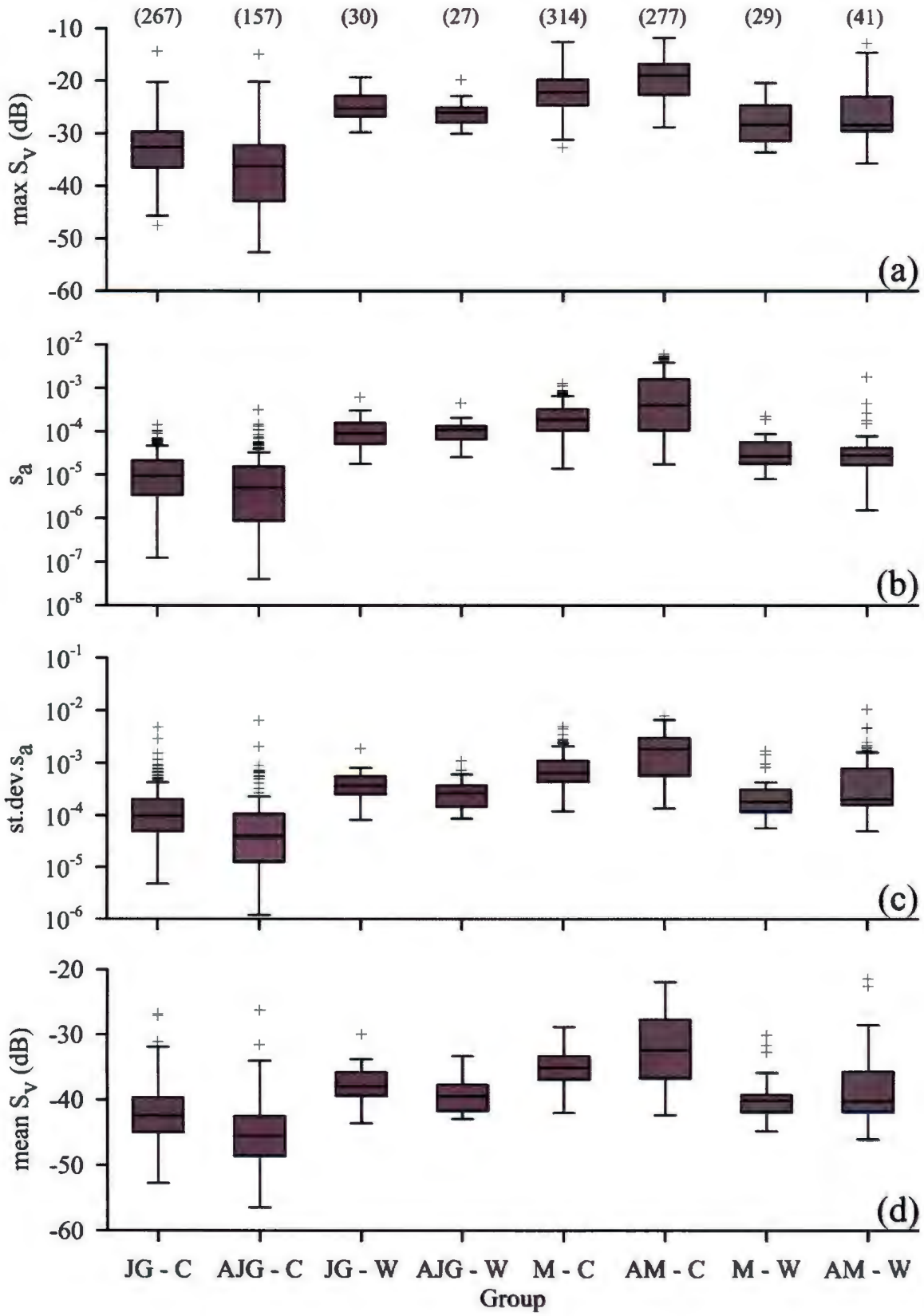
(267)
(157)
(30)
(27)
(314)
(277)
(29)
(41)
max S_V (dB)
-10
-20
-30
-40
-50
-60
(a)
s_a
10^{-2}
10^{-3}
10^{-4}
10^{-5}
10^{-6}
10^{-7}
10^{-8}
(b)
st.dev.s_a
10^{-1}
10^{-2}
10^{-3}
10^{-4}
10^{-5}
10^{-6}
(c)
mean S_V (dB)
-20
-30
-40
-50
-60
(d)
JG - C
AJG - C
JG - W
AJG - W
M - C
AM - C
M - W
AM - W
Group

Figure I.IV. Values of energetic parameters used in the optimal PDA model: max S_v (a), s_a (b), standard deviation of s_a (c), and mean S_v (d). Acoustic data were split into groups based on target type, use of acoustic data in optimal PDA and classification results: juvenile gadoids (JG), macrophytes (M), additional juvenile gadoids (AJG), additional macrophytes (AM); correctly (- C) and incorrectly (-W) classified samples. Capelin, AJG and AM were used to test the universal application power of the PDA algorithm developed using JG and M. The box is defined by lower and upper quartiles, center line is the median and caps indicate minimum and maximum values. Symbols (+) are outliers defined as: outlier < bottom of box - 1.5*difference between top and bottom of box, and outlier > top of box - 1.5*difference between top and bottom of box (Grapher 6. Golden Software Inc, Golden, Colorado, USA). Number of samples in each group are in brackets.